ARTHROPOD AND PLANT RESPONSES TO RESOURCE AVAILABILITY AND HETEROGENEITY

By

Irene Samantha Khavin

B.S., Rutgers University, 2001

Submitted to the Department of Ecology and Evolutionary Biology and the Faculty of the Graduate School of the University of Kansas
In partial fulfillment of the requirements for the degree of
Master's of Arts

_____
Bryan L. Foster

_____
Val H. Smith

_____
James Thorp

Date defended: _____

The Thesis Committee for Irene S. Khavin certifies
That this is the approved Version of the following thesis:

ATHROPOD AND PLANT RESPONSES TO RESOURCE AVAILABILITY AND HETEROGENEITY

Committee:

_____
Bryan L. Foster

_____
Val H. Smith

_____
James Thorp

Date approved: _____

Khavin, Irene S.
Department of Ecology and Evolutionary Biology, April 2008
University of Kansas

Arthropod and plant responses to resource availability and heterogeneity

Abstract

Species diversity has long been one of the central topics of ecological research, and there is still much uncertainty about the forces that generate and maintain diversity in communities. Abiotic factors such as resources, environmental conditions, and disturbances influence species composition; variation or heterogeneity in these abiotic factors is also hypothesized to affect diversity. Biotic interactions such as competition, mutualism, and predation further shape the composition of communities. Understanding what factors can influence diversity and community composition is important because knowledge of what maintains biological diversity in a particular habitat, taxon, or trophic level is the first step towards understanding how to preserve or to restore that diversity. Often, human activities disturb the natural cycling of nutrients and create physical disturbances, and the impacts of these changes are not sufficiently understood.

In this set of studies, the responses of plant and arthropod communities to experimental alterations of nutrient and disturbance regimes are explored. Three broad questions are addressed, along with aspects of their applicability to ecological management. 1) How does experimental manipulation of availability of nitrogen and phosphorus affect the composition and diversity of a grassland plant community – and what does this imply for restoration of native tallgrass prairie? 2) How do nutrient availability and disturbance interact to influence the arthropod community of a cool-season grass system – and how might this be important for management of cool-season hay fields? 3) How does nutrient heterogeneity affect the plant community and associated arthropod community of different herbaceous communities?

The first study, on experimental restoration of tallgrass prairie, shows that nutrient availability can strongly influence the plant community that develops over time at a site, and echoes previous studies that have shown that many native prairie plants are better suited to conditions of low availability of nutrients, especially nitrogen. The second study, which addresses the arthropod community of a cool-season hay field, shows that nutrient manipulation by fertilization strongly affects both the plant community, and the associated arthropod community. Meanwhile, the effects of haying disturbance on arthropods are subtle. A closer look at species and taxa of arthropods from this dataset shows that just as with plant species, different arthropod groups respond in dramatically different ways to changes in nutrient and disturbance regimes. Finally, the third study on the effects of heterogeneity leaves the question unanswered, as the time frame of the experiment appears to have been too brief to allow the treatments to take full effect.

ACKNOWLEDGEMENTS:

I would like to thank my advisors Dr. Bryan Foster and Dr. Val Smith for all the support and guidance that they have given me. My other committee members, Dr. Orley Taylor, Dr. James Thorp, and Dr. J. Chris Brown, have also been very helpful throughout my graduate studies. I thank Dean Kettle, Galen Pittman and Bruce Campbell for approving my study and providing logistical aid at the Nelson Environmental Studies Area; without their help it would have been impossible to accomplish this research. I'd also like to thank Dr. Robert Hagen for feedback on my research ideas, instructions and advice on insect sampling, and helpful resources for insect identification and data analysis.

I would like to thank my husband, Vladislav Khavin, for being wonderfully loving, supportive and not least for being very, very patient. My parents, Martin and Karin Karel, have been an inexhaustible resource of support, advice, and encouragement. I would also like to thank Beth Davis for many dinners and yoga sessions, Lisa Castle for coffee sessions and ping-pong, and all of the Gorgeous Biologist Knitters for many Thursday evenings well-spent among friends. In Dr. Foster's laboratory, I would like to thank Timothy Dickson, Erin Questad, Cheryl Murphy, and Cathy Collins for being excellent colleagues and friends, and for feedback on various papers, projects, and ideas. Also, Erin Questad deserves special thanks for performing the PERMANOVA analyses in Chapter 2, and Jennifer Moody-Weis and Tim Dickson helped with the set-up and take-down of one of the major field experiments. For the research presented in Chapter 1, Timothy L. Dickson

and Karl Anderson assisted with the collection of data; and Venessa Peterson initiated the experiment.

Finally, I would like to thank the organizations that provided me with financial support during graduate school: the National Science Foundation Pre-Doctoral Fellowship, the KU First-Year Fellowship, and NSF Grant DEB01-08302 to B. Foster and V. Smith. The following sources helped me fund my research: KSR Small Grants, and EEB and KU Graduate School travel funds.

TABLE OF CONTENTS

GENERAL INTRODUCTION:

A central goal of community ecology is to explain how biological communities are structured, and to predict how such communities respond to environmental change. Understanding the mechanisms that generate and maintain biological diversity in a particular habitat, taxon, or trophic level is the first step towards successfully managing that diversity, whether the intent is to preserve or to restore it. Both conservation and restoration become more crucial, and yet more difficult, as the pressures of human population growth on Earth's ecosystems becomes greater. The study of diversity's controlling factors is important because knowledge of what maintains biological diversity in a particular habitat, taxon, or trophic level is the first step towards understanding how to manage that diversity, whether the intent is to preserve or to restore it. Both conservation and restoration become more critical, and yet more difficult, as the pressures of human population growth on Earth's ecosystems becomes greater.

Species diversity has long been one of the central topics of ecological research, and there is still much to be learned about the factors that lead to more or fewer species in a community. The evolutionary processes of speciation and extinction are ultimately responsible for diversity patterns over large scales of time and space (Rosenzweig 1995). But at smaller temporal and spatial scales, ecological processes determine the numbers and identities of species that occupy a community. Abiotic factors such as resources, environmental conditions, and disturbances influence species composition; variation or heterogeneity in these abiotic factors is

also hypothesized to affect diversity (Tilman 1982, Naeem 1990, Hunter 1992, Tilman and Pacala 1993, Pacala 1994, Chesson 2000, Price 2002). Biotic interactions such as competition, mutualism, and predation further shape the composition of communities.

The first chapter of this thesis focuses on species diversity at the primary producer level, in the context of a tallgrass prairie restoration. Here, I analyzed the plant community response to addition or depletion of two key nutrients, nitrogen and phosphorus. This experiment addresses the following questions: 1) How does nitrogen addition affect plant species diversity, and the relative abundance of native tallgrasses and weedy species? 2) How does nitrogen depletion affect plant species diversity, and the relative abundance of native tallgrasses and weedy species? And 3) How does phosphorus addition, alone or in concert with nitrogen, affect plant species diversity, and the relative abundance of native tallgrasses and weedy species?

While ecologists have made great progress in understanding certain systems and processes, there are many questions yet to be answered and more yet to be asked. Terrestrial plant communities have been heavily studied, but terrestrial arthropod communities are far less well-known. Herbivorous insects are a useful study system because of their diversity and the complexity of their interactions with plants and with other trophic levels. In addition to being interesting for academic reasons, they are also important in their own right. In some systems, including some grasslands, insects eat more plant biomass each year than do vertebrate herbivores (Price 1997). They are a critical link in the cycling of nutrients and the flow of energy through

terrestrial systems. Insects are also important as both pests and mutualists in agricultural systems. The basic questions of what determines which species and how many species of arthropods are present, as well as the abundance of any particular species, are of both scientific and economic importance. Insects are an important group to study because they are abundant in all terrestrial ecosystems where plants are present, and may comprise up to 75% of the species diversity on Earth (Strong et al. 1984). They are also of considerable commercial importance in agriculture, as pollinators, predators, and pests (Price 1997, Raman 1997, Schoonhoven et al. 1998).

In Chapter 2, arthropod community data is collected from an experiment that imposes fertilization and haying treatments onto a cool-season Kansas grassland. This chapter explores the following questions: 1) How does fertilization affect arthropod abundance, species diversity, and community composition? 2) How does haying disturbance affect arthropod abundance, species diversity, and community composition? And 3) Is there an interactive effect between fertilization and disturbance that affect arthropod abundance, species diversity, and community composition?

The third chapters delves into the influence of nutrient resource heterogeneity on the arthropod community. Many ecological theories have proposed that heterogeneity can increase the number of species coexisting in a particular system; this study aimed to determine whether heterogeneity imposed at the elemental nutrient level can "cascade up" to the consumer level and affect the arthropod community. This experiment asks the questions: 1) How does (homogeneous)

nutrient addition affect arthropod herbivore diversity? 2) How do the effects of nutrient addition on arthropod diversity differ with the diversity and composition of the plant community to which the nutrients are added? 3) Does the effect of nutrient addition on arthropod diversity depend on whether the distribution of the added nutrients is homogeneous or heterogeneous? and 4) Does the effect of nutrient heterogeneity on arthropod diversity depend on the initial diversity of the plant community?

CHAPTER 1: EXPERIMENTAL MANIPULATION OF NITROGEN AND PHOSPHORUS AFFECTS THE ESTABLISHMENT OF TALLGRASS PRAIRIE SPECIES

CHAPTER SUMMARY

Soil nutrients are important determinants of plant community composition, and any habitat restoration depends on achieving an appropriate balance of such nutrients as nitrogen and phosphorus. Here we present results from the seventh year of a small-scale tallgrass prairie restoration experiment conducted near Lawrence, Kansas, USA. We used ammonium nitrate fertilizer and sawdust to modify soil nitrogen availability, and superphosphate fertilizer to increase available phosphorus in a subset of plots. We measured plant biomass, plant species richness, and percent cover of each species. We found that plant biomass increased monotonically with increasing nitrogen availability, while plant species richness exhibited a unimodal response to nitrogen manipulations. The nitrogen immobilization effect of carbon (sawdust) addition decreased species richness, but did not significantly affect native grass cover or weedy species cover. Phosphorus by itself affected only the abundance of native grass *Sorghastrum nutans*, but interactions between phosphorus and nitrogen influenced forb cover and the abundance of dominant grass *Andropogon gerardii*. Thus we demonstrate that nitrogen and phosphorus availability can affect the diversity and composition of grassland plant communities, and thereby play an important role in prairie restoration.

INTRODUCTION

Tallgrass prairie once covered a large portion of central North America. With the settlement of this region came intensive agriculture, which destroyed approximately 99% of the tallgrass prairie ecosystem (Samson and Knopf 1996). In recent decades, there has been increasing interest in restoring some of this lost habitat, with both private efforts and public programs such as the Conservation Reserve Program (CRP), a program administered by the USDA which encourages farmers to convert highly erodible cropland or other environmentally sensitive acreage to vegetative cover, such as native grasses. Efforts to restore native prairies have met with partial success, and helped to develop knowledge of prairie restoration techniques (Wilson and Gerry 1994, Packard and Mutel 1997, Copeland et al. 2002, Severns 2003, Van Dyke et al. 2004, Tix and Charvat 2005), but our understanding of how to restore prairies is not yet complete. While native prairies are floristically diverse, restoration sites are often marked by low diversity of native species, and invasion of ruderal and exotic plants (Packard and Mutel 1997).

Many factors can affect the re-establishment of a native prairie assemblage. Disturbances such as fire and grazing play an important role in establishing and maintaining diversity – helpful in the right frequency or intensity, but problematic if disturbances are too frequent or severe (Gibson et al. 1993). Likewise, either too little or too much of soil nutrients such as nitrogen and phosphorus can hinder the establishment of tallgrass prairie plant species (Blumenthal et al. 2003, Rothrock and Squiers 2003).

Nitrogen availability is often a limiting factor for plant productivity, but high supply rates of nitrogen can also lead to low species diversity. Commonly, the relationship between productivity and diversity is a unimodal curve (Grime 1979, Tilman 1982, Rosenzweig 1995). There are many proposed explanations for this pattern. On the increasing side of the curve, low availability of soil resources such as N and/or abiotic stress limits the number of species that can survive at low productivity. The peak in diversity occurs at moderate soil resource supply and productivity, and on the decreasing side of the diversity curve, increased soil resource supply might limit diversity by increasing competition for nutrients (Grime 1979); by shifting from competition for soil resources to competition for light (Goldberg and Miller 1990, Dickson 2006); or by resulting in more litter production, which prevents seedling establishment (Foster and Gross 1998). Weedy species, whether native or exotic, are often favored by high N availability (Huenneke et al. 1990, Bobbink et al. 1998, Smith et al. 1999). Native C_4 prairie tallgrasses are good competitors under low-N conditions (Wedin and Tilman 1990, Tilman and Wedin 1991, Turner and Knapp 1996). Soil availability of N can be reduced by the addition of carbon-rich materials like sawdust or sucrose; this stimulates soil microbial activity resulting in N immobilization (Killham 1994). This technique has been used successfully in some restorations to create a more favorable environment for native prairie species (Morgan 1994, Wilson and Gerry 1994, Baer et al. 2003, Blumenthal et al. 2003, Averett et al. 2004), although a few studies, especially in systems other than tallgrass prairie, have found mixed results of carbon amendments (Morghan and Seastedt

1999, Corbin and D'Antonio 2004). Previous studies suggest that carbon amendments might be useful in restoring tallgrass prairie lands degraded by intensive agricultural fertilizer use, or areas affected by atmospheric nitrogen deposition (Morgan 1994, Eschen et al. 2006).

The potential role of soil phosphorus as a determinant of plant productivity and diversity is less clear. In theory, if phosphorus and nitrogen are co-limiting, addition of phosphorus should shift the balance towards nitrogen limitation and favor vascular plant species that are superior competitors for nitrogen, or that can fix their own nitrogen (Tilman 1982). Phosphorus may also affect plant community dynamics indirectly, through mycorrhizal symbionts. Mycorrhizal growth is directly affected by soil N and P (Treseder and Allen 2002), and in turn influences plant community composition (Heijden et al. 1998, Smith et al. 1998, Hartnett and Wilson 1999). Mycorrhizae may be particularly important to native prairie grasses such as *Andropogon gerardii* growing in low-nutrient soils (Schultz et al. 2001). Nevertheless, to date there has been mixed experimental evidence that P additions can modify the productivity, composition, or species richness of grassland communities (Goldberg and Miller 1990, Gibson et al. 1993, Mamolos et al. 1995, Rothrock and Squiers 2003).

In the present study, we used small-scale experimental restoration in eastern Kansas to examine the effects of nitrogen and phosphorus availability on the re-establishment of tallgrass prairie species over a period of 7 years. Nitrogen and phosphorus treatments were combined factorially, providing the opportunity to detect

N x P interactions. We tested the hypotheses that 1) total plant diversity would be greatest in plots with reduced nitrogen (carbon amendments) and added phosphorus, creating the highest degree of nitrogen limitation; and 2) native prairie plant diversity and abundance would be greatest in plots with reduced nitrogen and added phosphorus.

MATERIALS AND METHODS

Study area

This experiment was established in March 1996 on an old-field site at the University of Kansas Nelson Environmental Studies Area, located northeast of Lawrence, KS. The area was used for grazing and agriculture until 1970, whereupon it was left fallow and only tilled periodically to remove woody vegetation. The soil is mapped as Grundy and classified as a Molisol with a silty clay loam texture. Prior to the start of the experiment, the plant community of the site was dominated by Canada goldenrod (*Solidago canadensis)*, common ragweed (*Ambrosia artemisifolia)*, giant foxtail *(Setaria faberii)*, poison ivy *(Toxicodendron radicans)*, common milkweed *(Asclepias syriaca)*, white sweet clover *(Melilotus alba)*, tall thistle *(Cirsium altissimum)*, and rough-leaved dogwood *(Cornus drummondii)*.

The site was prepared by disking and tilling to remove existing vegetation. Six native tallgrass prairie species were seeded into the plots: big bluestem *(Andropogon gerardii)*, little bluestem *(Schizachyrium scoparium)*, switchgrass

(Panicum virgatum), indiangrass *(Sorghastrum nutans)*, Illinois bundleflower *(Desmanthus illinoiensis)*, and prairie coneflower *(Ratibida columnifera)*.

Experimental Design

During the first growing season, only nitrogen was manipulated. A randomized six by nine grid was established, consisting of fifty-four plots, each 4 meters by 4 meters, with 1 meter walkways between plots. Nitrogen manipulations included a set of controls, two nitrogen depletion treatments (via carbon amendment), and six nitrogen enrichment treatments. Each treatment was replicated six times. The nitrogen depletion treatments received sawdust amendments of either 31.25 or 62.50 g m^{-2} yr^{-1}. Nitrogen enrichment treatments received commercial 34-0-0 ammonium nitrate fertilizer at one of nine supply levels: 1.0, 2.0, 3.4, 5.4, 7.5, or 9.5 g m^{-2} yr^{-1}.

Measurements of soil phosphorus levels during spring and fall sampling dates in 1996 and 1997 revealed that Bray P never exceeded 10 ppm in any of the experimental plots (Peterson 1998). These phosphorus levels are considered to be very low in the agronomic literature (Sawyer et al. 2002), suggesting possible P-limitation of plant productivity in this experimental system. Starting in the second year of the experiment, a phosphorus enrichment treatment was added to half of the replicates of each nitrogen treatment, in order to increase the intensity of N limitation and to explore possible N x P effects on plant productivity and species richness. Commercial 0-0-18 superphosphate (P_2O_5) fertilizer was applied at a rate of 11.25 g

m^{-2} yr^{-1} in order to double the available Bray P in the soil from its 1996-1997 average value of 5 ppm. Both N and P were applied in two equal doses: half in mid-May, and half in mid-June (see Peterson (1998) for further details).

The entire site was burned annually in the spring from 1997 until 2002 in order to prevent the invasion of woody shrubs and to inhibit the growth of cool-season species. Soil nitrogen availability is expected to have been reduced equally in all plots due to burn-induced nitrogen volatilization (Ojima et al. 1990, Seastedt and Ramundo 1990). The site was not burned in 2003, the year in which the data presented here were collected.

Sampling

In summer 2003, we surveyed all plots determine plant species diversity and abundance of each species. These surveys were conducted by searching the entire area of each plot, identifying the species present, and assigning percent cover values for each species found. To measure aboveground biomass, strips 8 cm wide and 300 cm long were clipped at soil level. The clipped vegetation and litter were brought back to the laboratory, sorted into live grass, live forbs, and litter. The material was then dried in an oven at 70° C for three or more days, and weighed to obtain dry mass.

Data Analysis

The data were analyzed with the statistical software package SPSS 14.0 and Minitab 15. We used factorial analysis of variance (ANOVA) to examine the effects of the nutrient manipulation treatments on plant biomass, species richness, species evenness, and percent cover of different groups within the plant community.

Linear and quadratic regressions were used to examine the relationships between plant diversity, percent cover, and nitrogen availability. It was not possible to perform regressions against N level *per se*, because it is not known how much nitrogen was removed from the pool of available soil N by the sawdust treatments. However, there is extensive experimental evidence (Morghan and Seastedt 1999, Baer et al. 2003, Blumenthal et al. 2003, Averett et al. 2004) that carbon additions effectively decrease available N, and we therefore assumed that soil N availability in the two sawdust treatments was lower than in the controls. Thus, we can compare the fit of a linear relationship between N and species richness with the fit of a quadratic relationship to determine which more closely described the observed trend. The exact N levels are uncertain in the two sawdust treatments, but it is reasonable to assume that they are in the correct rank order, i.e. the treatment with the most sawdust added had the lowest N availability. This being true, variation in their 'real' placement on the x-axis might change the shape of the curve, but not the fact that a curve is a better fit than a straight line.

We calculated species evenness based on the Simpson diversity index D; the evenness index used was (1/D)/S where S is species richness (Smith and Wilson 1996).

We further analyzed the plant community composition by breaking it down into groups of plants, and analyzing each group separately. We grouped different species in several ways: by functional group (grasses and forbs), native vs. exotic, and along a spectrum from conservative to weedy. To determine and analyze the restoration value of different plant species, we used their coefficients of conservatism (Swink and Wilhelm 1994). We also separately analyzed data for the three most dominant species: *A. gerardii*, *S. nutans*, and *S. faberii*.

We also tested whether sawdust addition had effects strong enough to be detected when separated from the nitrogen addition gradient. For each variable analyzed in Table 1, we performed an ANOVA with only treatments 1, 2, and 3 included. Treatments 1 and 2 were sawdust addition treatments, and 3 was a control – no nitrogen manipulation.

RESULTS

Total clipped plant biomass increased with increasing nitrogen supply (Table 1, Fig. 1, $R^2 = .144$, $p = 0.005$), but there was no significant difference in total biomass with and without phosphorus additions (Table 1).

Species richness showed a significant response to nitrogen manipulation (Table 1, Table 2, Figure 2A). The shape of the response across the experimental N supply gradient was quadratic rather than linear (Table 2). In N depletion treatments, species richness was lowest, and rose with moderate N amendment, then fell again with high levels of enrichment (Fig. 2A). To further examine the influence of the N

depletion treatments on this relationship we re-ran the analysis with these treatments removed (Table 3). These analyses showed that the sawdust treatments enhanced the fit of the quadratic curve, but that the unimodal shape was retained without the N-depletion treatments.

Species evenness was altered significantly by N manipulation (Table 1) and increased in a linear fashion across the N supply gradient (Fig. 2B). It was not significantly affected by phosphorus addition (Table 1).

Species diversity as measured by the Simpson's D index was significantly increased in a linear fashion by N addition, and there was no interaction between N and phosphorus (Table 1, Figure 2C). Phosphorus addition apparently decreased the effect of nitrogen manipulation across the entire depletion-enrichment spectrum.

Native grass cover decreased with increasing nitrogen supply (Table 1, Fig. 3A). No effect of phosphorus addition was found (Table 1). Exotic grass cover increased with N supply (Fig. 3B). Cover of weedy grasses and forbs increased with increasing nitrogen (Fig. 3C), and was unaffected by phosphorus addition (Table 1). Cover of forbs which could be considered conservative (coefficient of conservatism above 3) was negligible - they covered less than 1% of each plot; this includes native legumes (Fig. 3D). The three most dominant species were A. *gerardii*, *S. nutans*, and *S. faberii*. *Sorghastrum nutans* cover decreased with increasing N, but only in the presence of added P (Fig. 4A). *A. gerardii* or big bluestem was most abundant at lower N levels, but phosphorus addition reduced the magnitude of the difference

between N treatments (Table 1, Figure 4B). *Setaria faberii* cover increased with N, regardless of P addition (Fig. 4C).

The effect of sawdust addition compared with control plots was not significant for any of the variables presented in Table 1.

DISCUSSION

We demonstrate several interesting patterns of species diversity in this study. The first is an experimental example of the unimodal distribution of species richness. Many authors have postulated that the true relationship between productivity and species richness is the unimodal curve (Grime 1973, Tilman and Pacala 1993, Huston 1994, Rosenzweig 1995). This relationship is well known from observational data, especially from vascular plant communities (reviewed in Waide et al. 1999), but most experimental increases in productivity have shown only a decline in diversity (Gough et al. 2000, Mittelbach et al. 2001). It may be that this study was able to show a unimodal curve as a result of its longer duration (7 years) or because it involved a greater range of nutrient manipulation.

Also of interest is the observation that Simpson's diversity (D) and evenness show monotonic responses to nutrient manipulation, while richness shows a unimodal response. It seems that N enrichment increased evenness mainly by reducing the ability of native prairie grasses *A. gerardii* and *S. nutans* to exclude species that are good at taking advantage of excess N, such as *S. faberii* and an assortment of forbs. The improved evenness at higher N levels results in a higher diversity index despite a

lower species richness than at moderate N supply rates. Thus, at low N, prairie grasses are very dominant, while at high N, there is co-dominance by prairie grasses and 'weedy' grasses and forbs. The slope of Simpson's D is also moderated by phosphorus inputs; this effect appears to be a subtle one that is not evident from evenness or richness alone.

Our results are concordant with those of previous studies showing that high levels of soil nitrogen can be detrimental to the establishment of native prairie grasses and forbs, and instead encourage dominance of weedy grasses and forbs. In soils that are high in nitrogen, the addition of carbon in the form of sawdust or sucrose can reduce nitrogen availability and give C4 grasses a competitive advantage, thus helping to reduce weedy forbs and non-native grasses.

However, in soils with moderate to low nitrogen content, such as the soils at this site, it appears that additions of carbon can limit nitrogen levels enough to interfere with the growth of desirable prairie species as well as 'weeds.' Counter to our predictions, carbon amendment did not increase species richness or native tallgrass species dominance. Native grass cover was highest in plots without added nitrogen, but carbon amendment did not enhance native grass dominance (Fig. 3A). Similarly, cover of weedy species was equally low in control and carbon-amendment treatments (Fig. 3B, C). This and the unimodal pattern of species richness seen in our results (Fig. 2A) suggest that depending upon initial soil characteristics, carbon amendment may or may not improve the success of a restoration. In one carbon amendment study (Blumenthal et al. 2003), plots with the highest added C had eight

times the native plant biomass of untreated plots. In contrast, our results showed approximately equal cover of native grasses in the carbon-treated and control plots. Blumenthal et al. (2003) found that increasing levels of N addition without C addition did not increase weed biomass, suggesting that soil N availability was not limiting at that site, whereas in our study, N addition markedly increased weed abundance. Thus, different starting conditions of soil nutrient status yield different results when carbon amendment is used as a restoration technique. The high frequency of controlled burns used in managing this experimental restoration during 1997-2002 may have further reduced nitrogen availability and accentuated the effects of C addition (Ojima et al. 1990, Seastedt et al. 1991), but we can only speculate about the interaction between burning and carbon amendment because there were no unburned plots in this experiment.

The role of phosphorus in prairie restoration unfortunately remains unclear. Many prairie plants have mycorrhizal symbionts that help them obtain phosphorus (Smith and Read 1997), and that may be the reason these plants did not show a response to P addition in this experiment. It is also possible that although measured Bray P levels are low, P was not limiting for most plants at this site, regardless of their mycorrhizal status. In an earlier dataset from this experiment (Kincaid et al. 2002), P and N seemed to interact in determining prairie grass cover; tallgrass species were more abundant at high N levels without P than with added P. No such pattern was evident in *A. gerardii* two years later, but in *S. nutans*, P addition increased abundance at low N but not at high N supply levels. In a study by Gibson et al.

(1993) at Konza Prairie Research Natural Area, KS, phosphorus additions to mature tallgrass prairie did not significantly affect the abundance of any plant species; however, only 1 g m^{-2} yr^{-1} of P was applied, compared to the 11.25 g m^{-2} yr^{-1} used for this experiment. Similarly, Rothrock and Squiers (2003) found no effect of much larger P addition rates (13.8 g m^{-2} yr^{-1}) on the establishment of prairie species in an Indiana tallgrass prairie restoration. Willems et al. (1993) reported that in a Netherlands chalk grassland, P additions increased total aboveground productivity without decreasing species richness. Rangeland fertilization studies in a mixed prairie association in the Northern Great Plains (Black and Wight 1979) revealed that without P fertilization, application rates of 112, 336, and 1,008 kg N/ha significantly depressed plant tissue P levels for 2, 7, and >8 years, respectively. Goldberg and Miller (1990) found no significant effect of P addition to an annual plant community in Michigan. In contrast, Mamolos et al. (1995) found that additions of either N or P increased community productivity and altered plant species composition in a moderately acid lowland grassland in northern Greece. In hay meadows on peat soils in Somerset, United Kingdom, Kirkham et al. (1996) found that P was more important than N in determining both plant biomass production and species composition. Bardgett et al. (2006) studied 42L mesocosms containing mixed grassland communities on soils of three different residual fertilities, based primarily on soil P availability. In the treatment series that did not receive amendments with the facultative root hemiparasite *Rhinanthus minor*, plant species diversity was greatest in the lowest fertility soil. Thus, many factors can influence the plant

community's response to P addition, and it is not clear why our experiment showed a rather weak response to P.

The scant establishment of native prairie forbs suggests that these species are not limited by dispersal but by other factors such as competition. Only one of the several forb species added at the start of this experiment, *Desmanthus illinoiensis,* was still present after 7 years, suggesting that either initial seeding rates were insufficient or that the management techniques were not suited to encourage forb establishment. Intensive burning is known to favor C4 grasses at the expense of other species (Collins et al. 1995), and the annual burning schedule used in the early stages of this experiment is one possible cause for the lack of native forb establishment.

The techniques used to restore a prairie depend on the goal of the restoration, and the funding available. Seeding dominant native grasses and burning regularly appears sufficient to establish these grasses, which could restore many of the ecological functions of a tallgrass prairie (Baer et al. 2002, Camill et al. 2004). Re-creating the full diversity of a tallgrass prairie community from an impoverished seed bank would require more intensive management: more seed addition, and careful manipulation of nutrients and disturbances.

Table 1-1: Treatment effects on community and species measurements, evaluated with ANOVA.

	Nitrogen	Phosphorus	N*P
Total Biomass	**0.041**	0.520	0.996
Species Richness	**0.054**	0.721	0.304
Species Evenness	**0.0001**	0.480	0.577
Species Diversity (D)	**0.0001**	0.722	0.147
Native Grass Cover	**0.0001**	0.129	0.094
Exotic Grass Cover	**0.015**	0.366	0.981
Forb Cover	**0.0001**	0.354	**0.022**
Native Forb Cover	**0.0001**	0.258	**0.020**
Weedy Forb Cover	**0.0001**	0.160	0.080
Conservative Forb Cover	0.249	0.240	0.332
Andropogon gerardii Cover	**0.004**	0.640	**0.005**
Setaria faberii Cover	0.002	0.765	0.538
Sorghastrum nutans Cover	0.658	**0.022**	0.146

Table 1-2: Linear and Quadratic Regression of Species Richness vs. Treatment

Equation	R square	F	Significance
Linear	0.004	0.197	0.659
Quadratic	0.209	6.728	**0.001**

Table 1-3: Linear and Quadratic Regression of Species Richness vs. Treatment, N-reduction Treatments Removed

Equation	R square	F	Significance
Linear	0.039	1.632	0.209
Quadratic	0.186	4.453	**0.018**

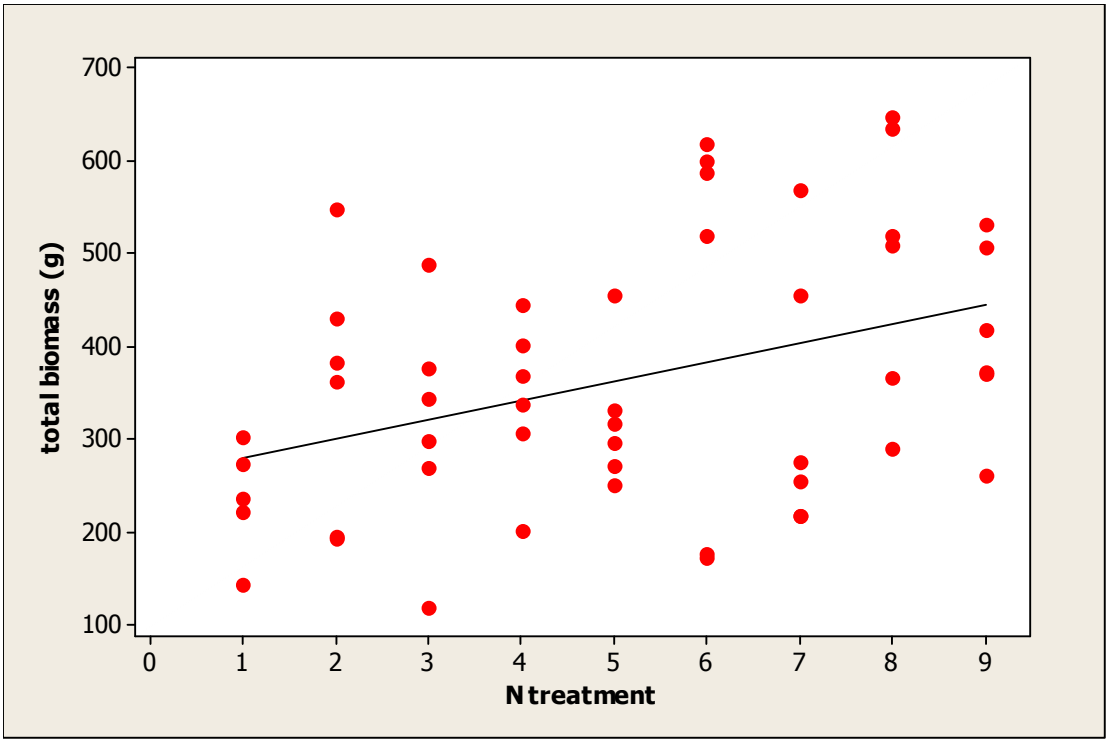
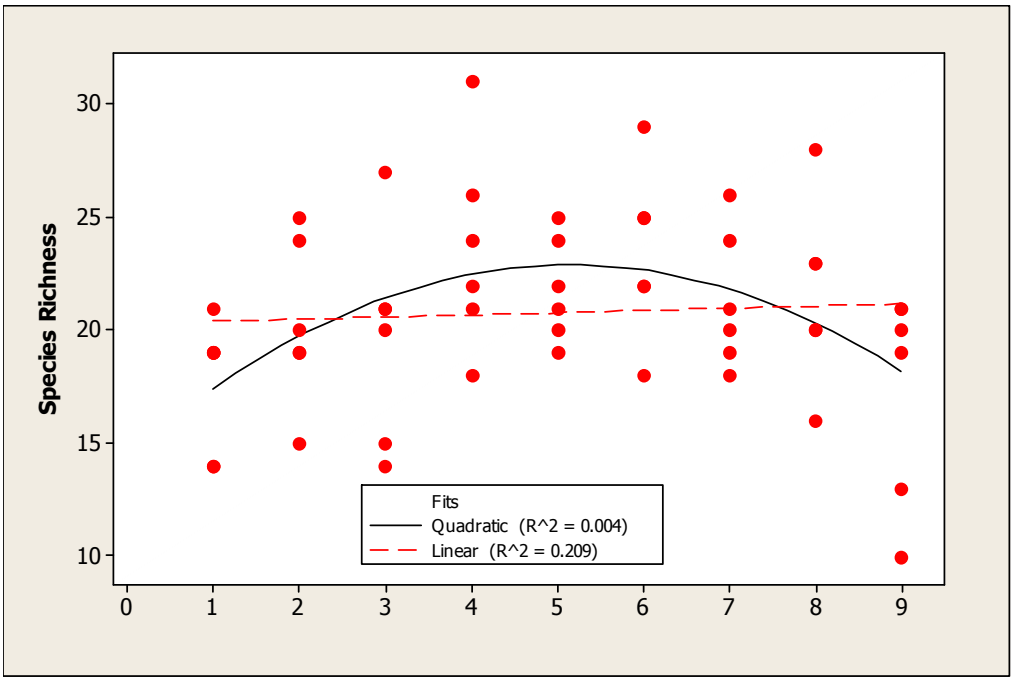
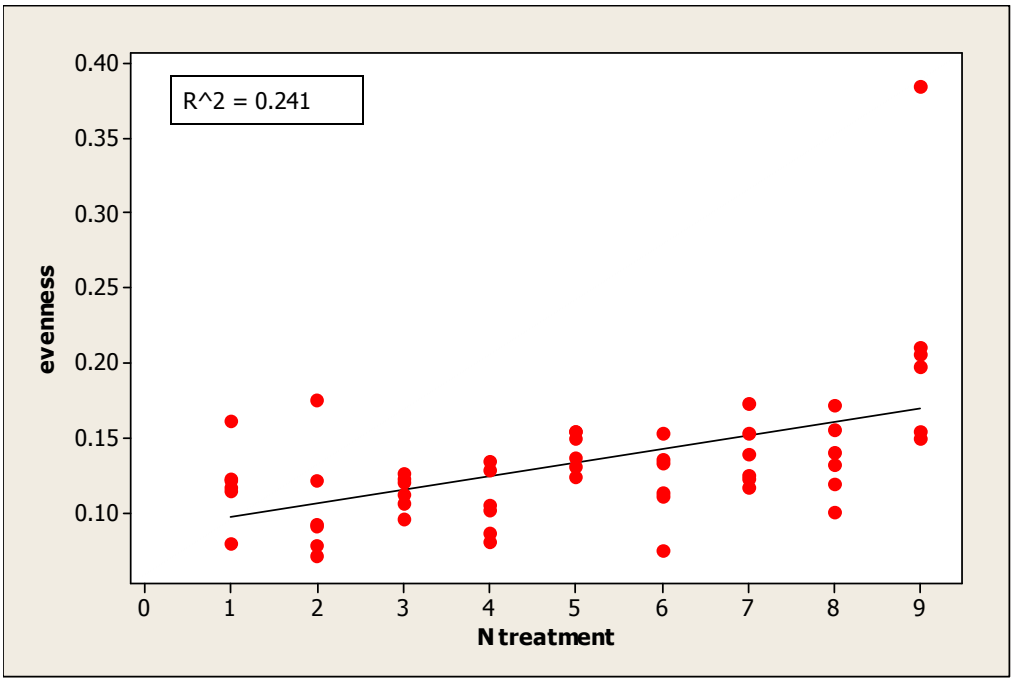


Figure 1-1: Plant biomass against nitrogen treatment.

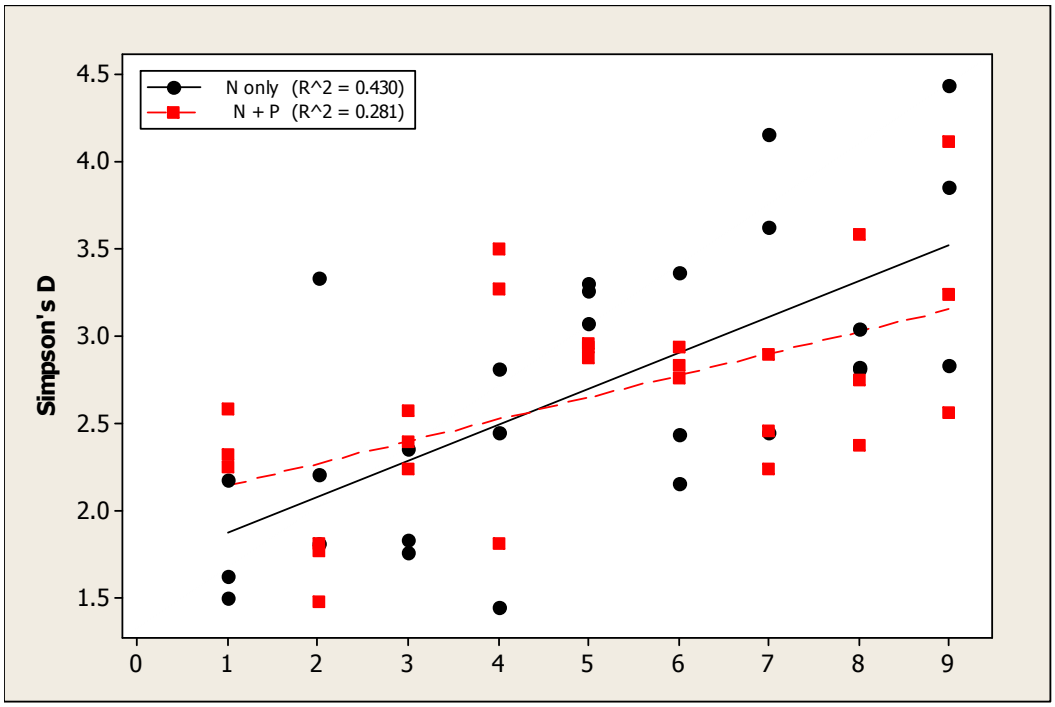
Figure 1-2: Plant species richness (A), evenness (B), and Simpson's Diversity (C) by nitrogen treatment.


Species Richness
30
25
20
15
10
0
1
2
3
4
5
6
7
8
9
Fits
Quadratic (R^2 = 0.004)
Linear (R^2 = 0.209)

1-2A.


R^2 = 0.241
0.40
0.35
0.30
0.25
0.20
0.15
0.10
evenness
0
1
2
3
4
5
6
7
8
9
N treatment

1-2B.


N only (R^2 = 0.430)
N + P (R^2 = 0.281)
Simpson's D
4.5
4.0
3.5
3.0
2.5
2.0
1.5
0
1
2
3
4
5
6
7
8
9

1-2C.

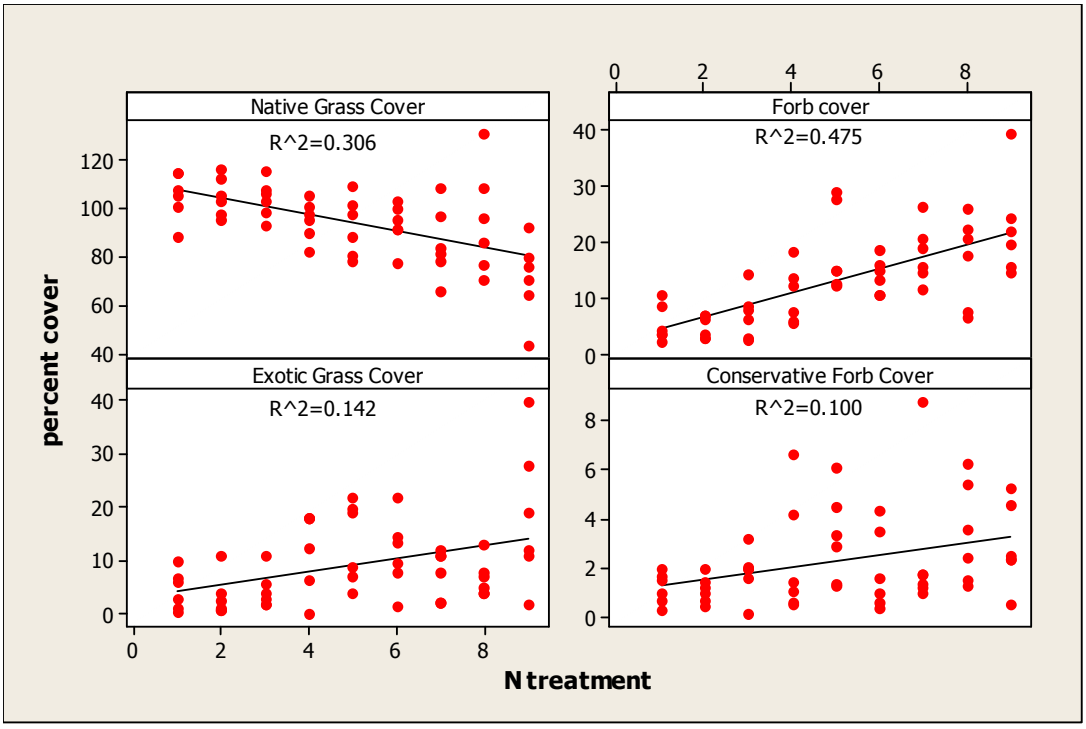
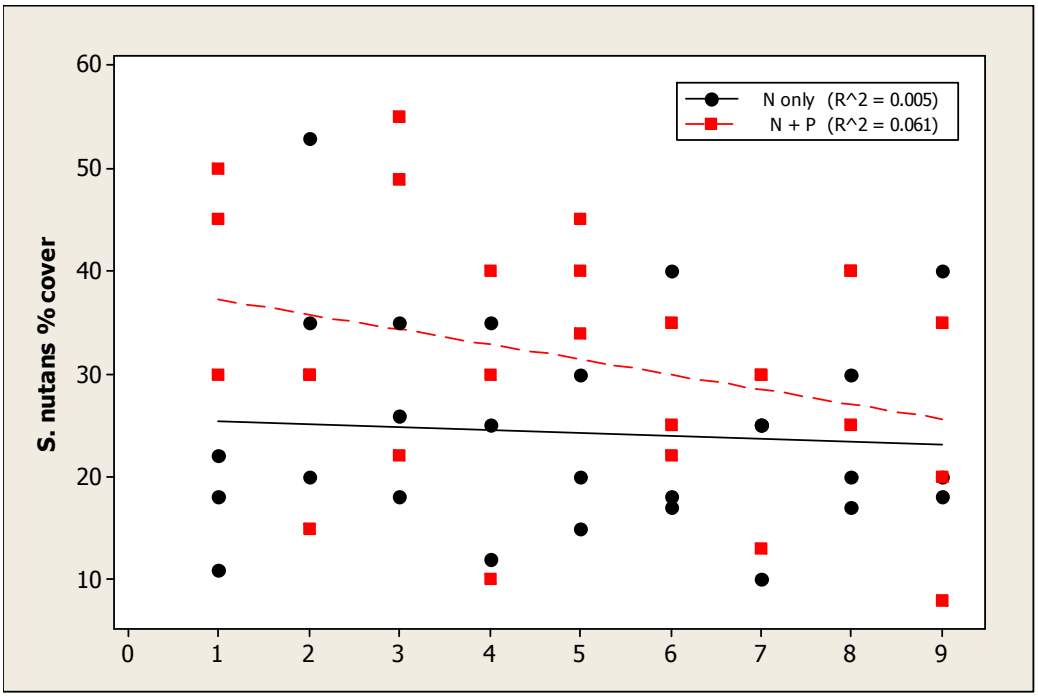
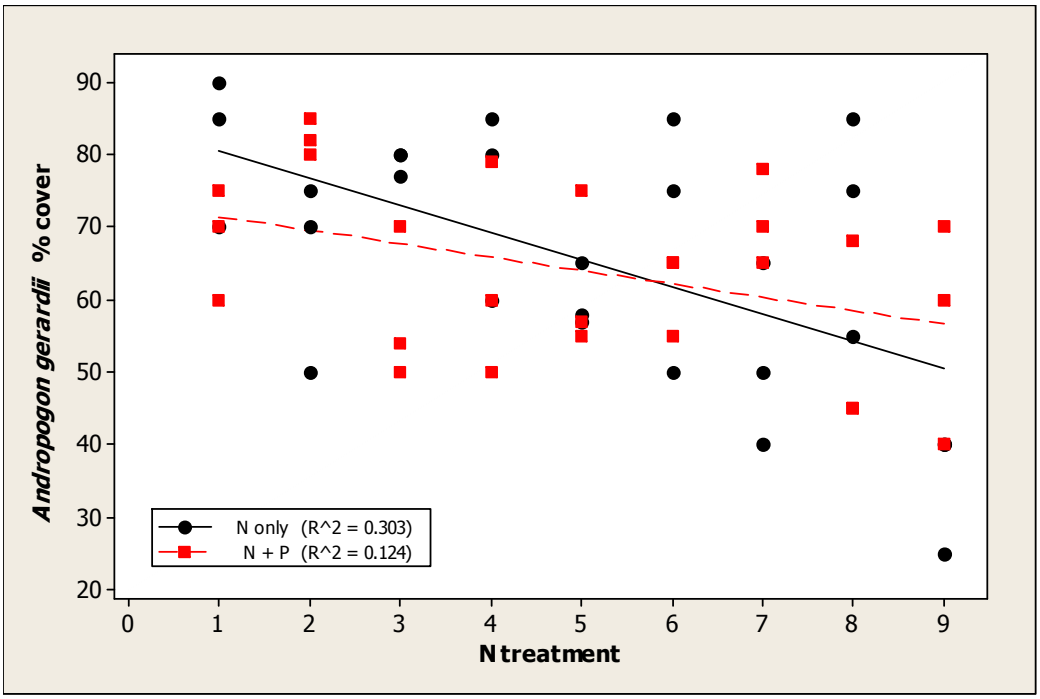


Figure 1-3: Native grass cover (A), exotic grass cover (B), forb cover (C), and conservative forb cover (D) by nitrogen treatment. Note that the scale of the Y axes is not the same in all graph panels.

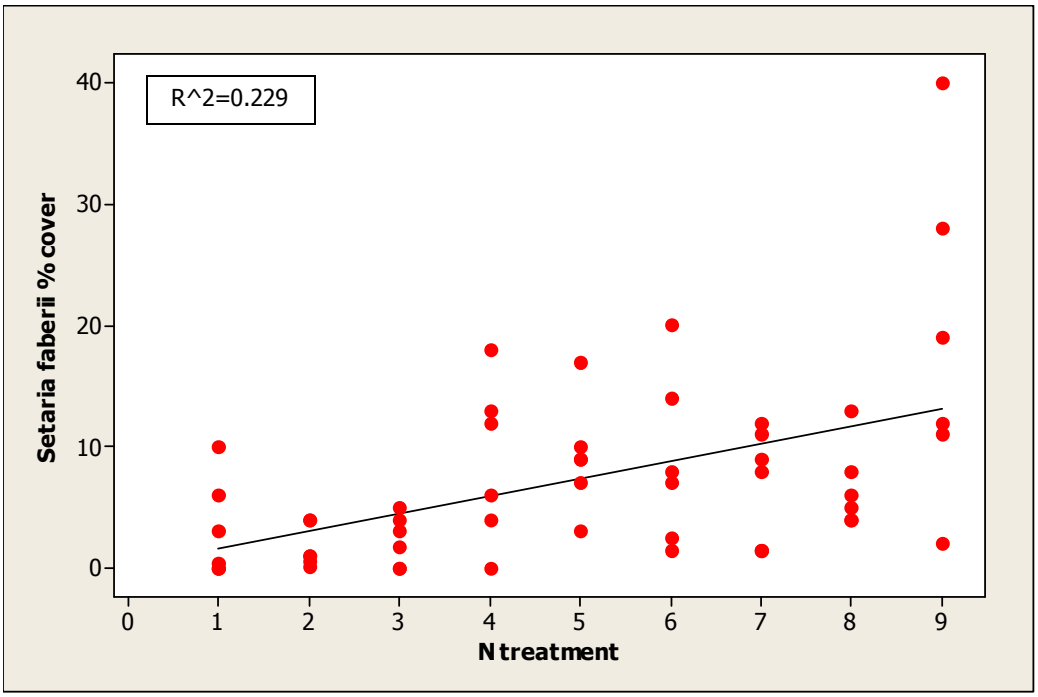
Figure 1-4: Percent cover of *Sorghastrum nutans* (A), *Andropogon gerardii* (B), and *Setaria faberii* (C). Note that the scale of the Y axes is not the same in all graphs.


S. nutans % cover
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
N only (R^2 = 0.005)
N + P (R^2 = 0.061)

1-4A.


Andropogon gerardii % cover
90
80
70
60
50
40
30
20
0
1
2
3
4
5
6
7
8
9
N treatment
N only (R^2 = 0.303)
N + P (R^2 = 0.124)

1-4B.


R^2=0.229
Setaria faberii % cover
N treatment
0
10
20
30
40
0
1
2
3
4
5
6
7
8
9

1-4C.

CHAPTER 2: ARTHROPOD COMMUNITY RESPONSES TO FERTILIZATION AND HAYING IN COOL-SEASON GRASSLAND

CHAPTER SUMMARY

The effects of fertilization and haying on cool-season grassland plant communities are well studied, but comparatively little is known about the impact of such management techniques on arthropod communities. I sampled arthropod communities at two time points during the 2003 growing season in a set of 32 experimental plots that had three years of factorial manipulations of fertilization and haying. I compared the arthropod community data with multiple measures of ecosystem function and plant diversity, including plant species richness, plant biomass, and NDVI. I found that fertilization increased arthropod abundance and decreased arthropod diversity, although it did not decrease arthropod species richness. The effect of fertilization on arthropod communities shifted during the growing season, so that in August there was a negative effect of fertilization on abundance and diversity, and a positive effect on biomass. Haying increased arthropod abundance, but did not affect arthropod richness or diversity. NDVI was strongly correlated with many plant community and ecosystem measures, and was a strong predictor of both arthropod abundance and arthropod diversity. In summary, this experimental data set demonstrates that 1) effects of management on grassland arthropods can be difficult to predict, in part because they vary substantially within a season and may be driven

by plant resources such as seeds or flowers, and 2) despite these sources of variability, NDVI is a potentially valuable tool for predicting arthropod diversity.

INTRODUCTION

Arthropod communities are shaped by many factors, but one of the most important is the plant community with which they are associated (Strong et al. 1984, Tscharntke and Greiler 1995, Jolivet 1998, Schoonhoven et al. 1998). Therefore, processes that affect the plant community, such as nutrient cycling and disturbance, influence the arthropod community as well (Siemann et al. 1998, Kruess and Tscharntke 2002a, b, Hartley et al. 2003, Schade et al. 2003, Debano 2006, Whiles and Charlton 2006). Some effects may be direct, for example a prairie fire may kill many insects and temporarily deplete the community. But the longer-term effects of the fire may have a positive effect on the insect community by increasing plant diversity and number of flowers (Fay 2003, Fonseca et al. 2005, Hartley et al. 2007). It is such longer-term shifts that "cascade up" to higher trophic levels that are of particular interest to many ecologists (Hunter and Price 1992, Knops et al. 1999).

Terrestrial food chains' response to nutrient enrichment is not as well studied as those in aquatic environments; it is well known that increased nitrogen deposition lowers plant species richness while it increases plant biomass (Tilman 1987, Huenneke et al. 1990, Foster and Gross 1998, Suding et al. 2005), but fewer studies have addressed the effects of nutrient enrichment on arthropod communities. In short-term experiments, increased nutrient availability has often increased arthropod

diversity (Hurd et al. 1971, Hurd and Wolf 1974, Kirchner 1977, Sedlacek et al. 1988) but in longer-term experiments, arthropod diversity tends to respond in the same direction as plant diversity, that is, it diminishes with increased nutrient enrichment (Haddad et al. 2000, Borges and Brown 2001, Perner et al. 2005, De Cauwer et al. 2006).

Disturbance sometimes promotes higher arthropod diversity (Fay 2003, Zurbrugg and Frank 2006, Hartley et al. 2007, Verdu et al. 2007), but sometimes it does not (Dennis et al. 1998, Jonas et al. 2002, Kruess and Tscharntke 2002b). Studies that have examined the responses of multiple arthropod groups have found that different taxonomic or different functional groups differ in their dependence on plant diversity and their response to resources and disturbance (Haddad et al. 2001, Jonas et al. 2002, Perner et al. 2005, Zurbrugg and Frank 2006).

Although multiple studies have addressed the effects of fertilization *or* disturbance of plant communities on their associated insect communities, few have combined these two important elements in a factorial experimental design. Here, I present results of arthropod surveys from an experiment situated in a cool-season Kansas grassland, which was designed to address effects of nutrient addition and disturbance by biomass removal on plant community composition. The arthropod dataset takes advantage of an established and ongoing experiment with plots of a size (10m x 10m) that facilitated arthropod sampling, and flyovers conducted to gather data on spectral reflectance of the vegetation allow the opportunity to explore the potential relationship between spectral reflectance and arthropod communities.

Hypothesis 1: Fertilization will increase arthropod abundance, and decrease arthropod diversity.

I predicted that arthropod diversity should be decreased by fertilization because fertilization decreases plant diversity. Many ecological models predict that a more diverse resource base should have a more diverse array of consumers because each kind of resource can potentially support specialist consumers (MacArthur 1972, Tilman 1986, Rosenzweig 1995). Lower plant diversity should decrease the number of different resources available to support a range of specialist arthropod herbivores, and in turn the specialist predators and parasitoids that feed upon the herbivores. Alternatively, however, there are other authors who have argued that increasing plant productivity should increase arthropod diversity by allowing scarce resources to become abundant enough to support additional species (MacArthur 1965, Abrams 1995); by allowing rare consumer species to become abundant enough to persist (Connell and Orias 1964, MacArthur 1965, Rosenzweig 1995); or by increasing intraspecific density dependence (Abrams 1995).

Hypothesis 2: Haying will reduce arthropod abundance, and mitigate the diversity-reducing effect of fertilization.

I expected haying to have two effects. The first is a dramatic reduction in the abundance and diversity of arthropods during the immediate aftermath of haying while plant biomass in hayed plots is minimal. This effect is assumed rather than tested in this study; I was more interested in a potential longer-term effect, seen earlier in the growing season prior to haying and when the C3 grasses are near peak

biomass in both previously-hayed and non-hayed plots. I expected this longer-term effect to be a mitigation of the diversity-reducing action of fertilization by allowing more plant species, and therefore more arthropod species, to coexist. This hypothesis is based on previous studies that have shown that certain types of disturbance, such as grazing (Gibson et al. 1992, Wallis De Vries et al. 2007) and fire (Hartley et al. 2007) can increase arthropod diversity, although the direction of the effect seems to depend on the intensity (Kruess and Tscharntke 2002a, Debano 2006) and seasonal timing of the disturbance, and also on concurrent disturbances such as drought (Fielding and Brusven 1995). I predicted that unfertilized hayed plots would be similar in arthropod abundance and diversity to unfertilized non-hayed plots – in other words, that the effect of haying would depend on fertilization because in general, the effect of removing biomass should be greater when there is more biomass to remove (i.e. in fertilized plots) and in this particular system, previous data shows that the TINDVI and thus primary productivity of fertilized hayed versus non-hayed plots was much more different than unfertilized hayed versus non-hayed plots, and the difference in plant diversity caused by haying was much greater in fertilized than in unfertilized plots (Foster et al. submitted).

To help elucidate the underlying reasons for the responses of the arthropod community to fertilization and haying treatments, a variety of ecosystem and plant community variables will be analyzed to determine their possible relationship with the arthropod community. These variables will include TINDVI, plant biomass, plant richness, plant species evenness, % C, % N, and number of grass seedheads per plot.

MATERIALS AND METHODS

Study Site

The experimental plots are located 12 kilometers north of Lawrence, Kansas, USA (Kettle and Whittemore 1991) at the Nelson Environmental Study Area (Jefferson County, 39˚03′ N, 95˚12′ W) in a former pasture/hay field. This tract of land is in the deciduous forest-tallgrass prairie ecotone, and consists of undulating ridge-to-swale geomorphology. The soil is Pawnee clay loam (fine, montmorillonitic, mesic Aquic Argiudolls), formed from glacial deposits of loess and till with weathering of interbedded limestones and shales (Kettle and Whittemore 1991). The mean annual precipitation is 930 mm and the mean annual temperature is 12.9˚C (Atmospheric Science Library 1990).

The field in which this study is located has had a long history of cultivation, but was last used over 20 years ago for cool-season hay production and grazing. Since then it has been maintained as open cool-season grassland by regular mowing to prevent invasion by woody plants. Before the establishment of this experiment, the field was last mown in 1998. At the start of this study, the experimental site was dominated by the C_3 grasses introduced for hay production, primarily *Bromus inermis* and *Lolium arundinacea*. Other abundant grasses include *Poa pratensis* (introduced C_3 grass) and *Andropogon virginicus* (native C_4 grass). Common forbs at the site include *Oxalis stricta* and *Solidago canadensis*.

Experimental Design

The experimental plots (Fig. 1) were established in March of 2000 by establishing a 4 x 4 grid of 16 10 x 20 m plots at the site. Plots were separated by 3 m buffer strips. Each plot was divided into two contiguous 10 x 10 m subplots for a total of 32 subplots. A split-plot design with a 2 x 2 factorial set of treatments was assigned to the experimental: two levels of nutrient fertilization (fertilized; not fertilized) were applied as the whole-plot factor and two levels of haying (hayed; not hayed) applied as the split-plot factor.

In plots with the fertilization treatment, NPK fertilizer (29-3-4) was distributed by hand at a rate of 14-16 g N/m^2 per year. This application rate is within the upper part of the range typically applied to production cool-season hayfields in this region (Murphy 2004). In 2000, 2001 and 2002, fertilizer was applied in two doses: 8 g N/m^2 in early April and 8 g N/m^2 in either late May or early June. In 2003, one application of NPK at a rate of 14 g N/m^2 was applied in mid-April. Each year the appropriate subplots were hayed in mid-June as is typical for the cool-season hayfields of the region. Haying involved mowing the vegetation to near-ground level and removing the resulting thatch.

Vegetation sampling and processing

Aboveground plant biomass was sampled in mid-June 2003 in the experimental plots, just before haying and during the peak of biomass production for cool-season grassland. In each subplot, two 0.8 x 2 m strips of biomass were clipped to ground level with electric clippers. All biomass and litter within the strip area was

collected, and each sample was separated into live and litter fractions. The live fraction was further sorted to species. All biomass was dried to constant mass at 74˚C in a forced-air oven and then weighed. After weighing, the entire live fraction was ground to powder and analyzed for live plant tissue carbon (C) and nitrogen (N) content using a CHN Combustion Analyzer (Carlo Erba, Milan Italy). Also in mid-June before haying, all plant species present within each 10 x 10 m subplot were surveyed to provide a robust estimate of subplot species richness.

Arthropod sampling and processing

Arthropod samples were collected in mid-June 2003, just prior to haying and timed to correspond with the collection of plant data, and again in August 2003 to examine seasonal variations in arthropod response to treatments. Samples were collected with a muslin sweep net, while walking in six transects across each 10 x 10 m subplot. Each transect received a sampling effort of 25 sweeps. After each transect, the contents of the sweep net were transferred to a jar with ethyl acetate as a killing agent, and then each sample was placed into a zip-lock bag and frozen at -20°C. Later, samples were thawed and processed: plant material and detritus were removed, and arthropods were sorted to species or morphospecies (Oliver and Beattie 1996) and counted to produce arthropod abundance data. After sorting, identification, and counting, arthropods were dried for at least 3 days in a 70°C oven, and then weighed to obtain dry weight (biomass). To improve the reliability of species and morphospecies designations, a collection of voucher specimens of all species was

kept. Sampling by sweep net provides a broad selection of arthropods, but there are some biases produced. This method emphasizes vegetation-dwelling arthropods and is therefore good for studying relationships between plant and arthropod communities, but it under-represents other groups: fast-flying aerial insects, litter-layer dwellers, leaf and stem borers, and soil arthropods.

Spectral reflectance and light interception

During the growing season of 2003, remotely-sensed spectral reflectance data were collected from over-flights of the plots on ten different dates, approximately every 20 days between April 12 and October 28. Over-flights were conducted at an altitude of 3200 m ASL. Aerial imagery was captured using a DuncanTech MS 3100 digital multi-spectral camera mounted in a single engine light aircraft. The camera captures data in the red (630-690 nm) and near-infrared (760-900 nm; NIR) spectral bands. To convert raw data to units of absolute radiance, correction coefficients were generated by imaging a calibrated light source with varying neutral density filters and camera settings (Schiebe et al. 2001). These corrected data were then used to calculate the Normalized Difference Vegetation Index (NDVI; (Rouse et al. 1974)). NDVI is calculated using the formula NIR - Red/NIR + Red. This normalizing index corrects for seasonal and diurnal differences in sun angle and is resistant to the influence of haze and atmospheric aerosols. To optimize the consistency of our data set, all images were flown on clear days between 10:00 AM and 3:00 PM. The end

result of the 2003 flyovers was an NDVI data set containing seasonal time-series of vegetation greenness for each of the 32 subplots.

Data Analyses

Time-integrated NDVI - TINDVI is used as a proxy for plant productivity over the entire growing season. Using NDVI data from the ten sample dates in 2003, the seasonal time-integral of NDVI (TINDVI) for each subplot was computed using a trapezoidal approximation.

Diversity Indices - Species richness (*S*), community evenness (*E*) and Shannon diversity index (*H′*) were calculated for both plants and arthropods. Plant richness was evaluated as the total number of plant species recorded in a subplot. Arthropod richness was evaluated as the total number of species and morphospecies collected in a subplot's sweep net sample. *H′* was calculated as $-\Sigma\, p_i \times \log (p_i)$ where *p*i is the proportional abundance represented by a given species or morphospecies in a subplot. Plant diversity (*H′*) was calculated using the biomass of all plant species recorded in a subplot sample. Arthropod diversity (*H′*) was calculated using the number of individuals of each species and morphospecies in a subplot.

Analysis of variance (ANOVA) – Factorial ANOVA was used to evaluate treatment effects on diversity indices, arthropod density and ecosystem variables. All NDVI and biomass data were $\log_{10}$ transformed to meet the assumptions of ANOVA.

Permutational analysis of variance (PERMANOVA) – In order to assess the effects of treatments on the overall composition of the arthropod community,

permutational analysis of variance was used. This non-parametric technique is designed to work with ecological data sets that violate many of the assumptions of MANOVA, and that are drawn from multifactorial experimental designs (Anderson 2001). The data were analyzed using both species numbers and species biomass, because it is not obvious which measure of abundance is more ecologically relevant. The analysis was performed using the PERMANOVA software (Anderson 2005). Non-metric multidimensional scaling (NMDS) was used to generate a scatterplot of Bray-Curtis distances between the arthropod community compositions of plots under different treatments.

All other statistical analyses were performed using Minitab (version 15.0).

RESULTS

Ecosystem and Plant Community Responses

The productivity and species composition of the plant community responded in multiple aspects to the experimental treatments. Living plant biomass was highest in fertilized non-hayed plots, followed by fertilized hayed plots, then non-fertilized non-hayed plots, and finally non-fertilized hayed plots (Table 1). TINDVI, which is a robust general substitute for many ecosystem variables (Foster et al.) is higher in fertilized plots and lower in non-fertilized plots (Table 1). The number of grass seedheads present at the time of the June vegetation clipping was highest in plots that were hayed in the previous year, especially in fertilized hayed plots; there was an interaction between fertilization and haying treatments (Table 1). Plant species

richness, evenness, and Shannon Diversity (H') all were highest in unmanipulated plots, but these measures of the plant community were differently affected by the treatments. Species richness was reduced by fertilization, but this effect was much smaller in plots that were also hayed (Table 1, Fig. 2a). Evenness was not significantly influenced by either treatment alone, but by the interaction; haying reduced plant species evenness in non-fertilized plots, but increased it in fertilized plots (Table 1). Shannon Diversity (H') was directly deceased by fertilization, and was also affected by an interaction between fertilization and haying (Table 1). Leaf % C and % N were both increased and the C:N ratio was decreased by fertilization (Table 1), but plant tissue chemistry was not significantly influenced by haying.

Arthropod Community Responses

The effects of fertilization and haying treatments on arthropods were dependent in part on the season during which samples were collected. Samples from August were only of non-hayed plots because the plant biomass had not recovered from the June haying and thus sweep sampling in those plots would have yielded very few arthropods.

Arthropod abundance, or the number of individuals in a sample from a particular plot, responded positively to fertilization in June, but negatively in August (Table 2). This pattern is unchanged if mowed plots are excluded from the June dataset so that the same set of plots are being compared. Arthropod biomass

increased in response to fertilization in June, but showed no significant response in August (Table 2).

Total arthropod species richness showed no response to fertilization or haying in June, but showed a significant decrease in response to fertilization in August (Table 2). Arthropod Shannon diversity (H') was higher in unfertilized plots than in fertilized plots in both June and August, although for different reasons – in June, fertilized plots had many more individuals than unfertilized plots, but the same number of species, and therefore lower evenness. In August, fertilized plots had fewer species and fewer individuals; their evenness was the same as for unfertilized plots, but overall diversity was lower because of reduced species richness.

Analysis of overall community composition with PERMANOVA (Table 5a-6b) shows that although species richness did not respond to fertilization or haying, there were significant shifts in community composition. Analyses performed on counts of individual species showed that fertilization and haying each significantly changed the arthropod community, but there was not a significant interaction between them (Table 5a). Analyses using the biomass of each species as a measure of abundance showed that the individual factors and their interaction were significant according to PERMANOVA ($p = 0.001$) but haying and the fertilization-haying interaction were nonsignificant according to the stricter Monte Carlo test of significance. Because almost all of the permutation values were unique, it is probably reasonable to use the PERMANOVA p-value instead of the Monte Carlo p-value.

The PERMANOVA, in addition to performing overall analysis of the interplay between factors, also includes *a posteriori* tests that take a closer look at the relationships between each factor within levels of the other factor. Based on counts of individuals, in non-hayed plots there were significant differences ($p = 0.002$) between fertilized and unfertilized plots. In hayed plots, too, the communities of fertilized and unfertilized plots were significantly different ($p = 0.001$). In unfertilized plots, the difference between hayed and nonhayed communities was not significant, but in fertilized plots there was a significant difference between hayed and nonhayed ($p = 0.002$). The pairwise comparison results were similar when analyses were performed using species biomass data. To visualize the distances between communities in different treatment combinations, an NMDS scatterplot of Bray-Curtis distances drawn from species count data is shown in Figure 2. As the various other analysis techniques show, there is a clear separation between fertilized and unfertilized arthropod communities. There appears to be some separation between hayed and nonhayed communities in fertilized plots, but in unfertilized plots, the values overlap.

Arthropod responses by taxonomic orders and selected species

In June arthropod samples, different taxonomic groups showed widely divergent responses to experimental treatments. Grasshoppers (Orthoptera) were more abundant in hayed plots, but their numbers were not affected by fertilization. Their species richness, however, was higher in unfertilized plots (Table 4a). Spiders

(Arachnida) were also more abundant in hayed plots, but fertilization seemed to have no effect on their numbers or diversity (Table 4a). Beetles (Coleoptera) were affected by both fertilization and haying, and there was an interaction. Fertilization or haying alone had only a moderate effect on their numbers, but fertilization and haying together resulted in a large increase in beetle abundance. This interaction was caused by the response of one species, coded D12, which responded strongly to the combination of haying and fertilization. Excluding this species from the analysis of variance eliminates the significant interaction of haying and fertilization, but each factor alone still produces a significant effect on the remaining species' abundances. Beetle richness was increased by haying, and unaffected by fertilization (Table 4a). True bugs (Heteroptera) were also affected by both haying and fertilization, and their interaction – again, plots that were both hayed and fertilized had a much greater abundance of true bugs. This effect was driven mainly by one species, designated F10. Exclusion of this species left the effect of haying intact, but eliminated the effect of fertilization, and the interaction between fertilization and haying. The richness of Heteroptera was significantly increased by both fertilization and haying (Table 4a). Planthoppers, leafhoppers, and aphids (Homoptera) were not numerically affected by the experimental manipulations, but their richness was greater in unfertilized plots (Table 4a). The abundance of bees and wasps (Hymenoptera) was increased by fertilization and haying, and also by an interaction between fertilization and haying. Most of these effects appear to have been driven by two species, "B03" and "B31", but there was still a significant effect of haying, and of the fertilization x

haying interaction, with these two species removed from the analysis. The species richness of bees and wasps was not significantly affected by either treatment (Table 4a). The abundance of flies (Diptera) was increased by fertilization; one species "G05" showed a particularly strong response to fertilization but was unaffected by haying. Removal of this species from analysis, however, reveals that the rest of the Diptera not only responded to fertilization, but there was also a fertilization x haying interaction such that fertilization only slightly increased Diptera numbers in hayed plots, but dramatically increased the abundance of Diptera in non-hayed plots. Or, to state it another way, haying appeared to nullify most of the effect of fertilization on Diptera abundance. Species richness of Diptera was not influences by treatments (Table 4a).

In August 2003, some taxonomic groups were much less dominant than they had been in June, and responses of each group were somewhat different. Beetles, true bugs, and flies were scarce, and because of their low numbers were not analyzed separately. Grasshoppers (Orthoptera) were abundant, but neither abundance nor richness was affected by fertilization, nor did any of the dominant species within the order show a patterned response to experimental treatment (Table 4b). Spiders (Arachnida) were more abundant and more diverse than they had been in June, and although spiders as a whole did not show a significant response to fertilization, two of the dominant species showed opposite responses – "S03" was more abundant in unfertilized plots, while "S16" was more abundant in fertilized plots. Planthoppers and leafhoppers (Homoptera) were more abundant and also more diverse in

unfertilized plots; removing the two dominant species ("C11" and "C12") still left a significant response to fertilization in the remaining species. Bees and wasps were much less numerous and less diverse in August than in June, and showed no significant response to fertilization (Table 4b).

Relationships between ecosystem/plant variable and arthropod responses

A correlation matrix (Table 3) was created to determine which ecosystem and plant community variable were most strongly correlated with the responses of arthropods, and also which plant and ecosystem variables were most closely correlated with each other. Arthropod data from June was used because it provides the most complete dataset, and also corresponds best with the timing of plant biomass and plant diversity data collection; arthropod data from August was not included in this analysis because it only includes samples from non-hayed plots, and therefore is less complete. TINDVI was correlated very strongly (correlation coefficient > .7, $P < 0.001$) with all plant community and ecosystem variables except for number of seedheads per plot. Arthropod biomass was positively correlated with TINDVI, and arthropod abundance was positively correlated with TINDVI and number of seedheads per plot (Fig. 3 A, B). Arthropod species richness was not significantly correlated with any plant or ecosystem variable, but arthropod diversity (H') was negatively correlated with TINDVI and number of seedheads per plot (Fig. 4 A, B).

DISCUSSION

In this study, arthropod community dynamics were determined not only by the experimental manipulations, but also by the month in which samples were collected. The treatments applied to the experimental plots yielded different effects on arthropods in early summer and late summer. Other factors that can affect arthropod diversity include light regime and soil moisture (De Cauwer et al. 2006).

For this particular system, much of the difference in community responses from June to August can be explained by an event that takes place in June, namely, the flowering of the cool-season grasses *Bromus inermus* and *Festuca arundinacea*. These two grasses dominate many of the plots in this experiment, and when they flower, this attracts a large quantity of small Diptera, primarily the bromegrass seed midge *Contarinia bromicola* (Curry et al. 1983), which is likely to correspond to morphospecies G05 in this dataset. Both the midges and the grass seeds themselves attract an assortment of parasitoid and seed-feeding Hymenoptera in the superfamily Chalcidoidea (Soroka and Nerland 1992), corresponding to morphospecies B03 and B31 in this experiment. This affected the evenness of species in the June samples, because the number of arthropod individuals was nearly an order of magnitude larger, while the number of species present per sample was only slightly larger. The dominance of these brome and fescue specialists was greatest in plots with the most seedheads, which generally were subplots that were both fertilized and hayed (Fig. 2 D). These species, in turn, apparently increased the number of other predatory

arthropods, including spiders, and the insidious flower bug *Orius insidiosus*, morphospecies F10, which feeds on the eggs and larvae of numerous insects.

In August, by contrast, the beetles, true bugs, and flies were scarce, and the arthropod community was strongly dominated by grasshoppers, spiders, and leafhoppers/planthoppers. Few individual species could be picked out as responding to fertilization treatment, which is not surprising because the strongest effects of fertilization on plant biomass, tissue quality, and other plant resources were probably observed in June when fertilizer had been more recently added and cool-season grasses were at their peak.

I had predicted that arthropod diversity would decrease with fertilization and would respond positively to haying disturbance, while arthropod abundance would do the opposite. However, the results of this experiment, while partially agreeing with studies showing a decrease in diversity in response to fertilization (Haddad et al. 2000, Perner et al. 2003, Hartley et al. 2007), suggested that the effect is not consistent throughout the growing season, and depends on the metric used to assess arthropod diversity. Arthropod richness only decreased in response to fertilization in August, not during the period of peak plant biomass and arthropod abundance in June. H', a measure that incorporates both richness and evenness, did decrease with fertilization in both June and August. As described above, this can be tied to the seedhead effect: increased numbers of seedheads in fertilized plots increased the density of arthropods without significantly changing the number of species, thereby decreasing overall diversity by decreasing evenness.

The prediction that haying would mitigate the decrease in arthropod diversity resulting from fertilization (paralleling the pattern of plant species diversity) was not supported by this dataset, because there was no significant difference in either richness or H' between hayed and non-hayed plots. Although haying did not affect arthropod diversity, it did affect arthropod density because hayed plots had more seedheads than their non-hayed counterparts, regardless of whether or not they were fertilized.

Overall arthropod community composition in June was strongly influenced by fertilization and by haying, as the results of the PERMANOVA and NMDS analysis show. It is interesting that this pattern holds true whether number of individual arthropods or biomass is used as the measure of arthropod abundance. Because the large numbers of Diptera and Hymenoptera in plots with flowering grasses did not increase the biomass of each sample by much (each individual being very tiny) I would have expected that these two measures would show different patterns of community composition. The fact that they do not, implies that it was not only grass-seedhead attracted arthropods that changed in response to experimental conditions, but merely that they supplied the most obvious and measurable change. The suggested implication of the similarity between the two measurements is that even without the obvious numerical changes of the small flies and wasps associated with grass seedheads, the overall community did change in ways that would not be measurable without multivariate analysis.

The strong relationship between TNDVI and arthropod diversity was among the most interesting results of this study. TNDVI is an index that integrates many aspects of the nature and status of a plant assemblage, including plant tissue chemistry, biomass, canopy interception of photosynthetically active radiation, and plant diversity (Gould 2000, Fairbanks and McGwire 2004, Foster et al. submitted). Elsewhere, NDVI has also been used to estimate crop water stress (Clay et al. 2006) and CO_2 flux (Wylie et al. 2007), demonstrating the broad application of this index. NDVI has been used to monitor insect pest outbreaks in agricultural crops (Grilli and Gorla 1997, Sudbrink et al. 2003, Board et al. 2007) or forests (Coops et al. 2006), and Lassau et al. (2005) found that NDVI could predict ant community composition differences in open-canopy forest in Australia. However, few other studies have evaluated its relationship with arthropod diversity, and therefore little is known about its potential use as a predictor of arthropod community composition in natural or semi-natural grasslands. This experiment is one of the first to demonstrate a strong link between arthropod diversity and NDVI. The use of TINDVI in analyzing the arthropod data from this study helps to demonstrate a negative relationship of arthropod diversity to primary production. Some authors have postulated that more primary productivity should support more arthropod individuals and thus perhaps more species (Hurd et al. 1971, Hurd and Wolf 1974, Kirchner 1977, Vince et al. 1981, Siemann 1998a), but others have argued that the reduced diversity generally associated with increased productivity (especially by artificial means) should decrease the number of resources for arthropod specialists, and thus reduce the

diversity of the arthropod community (Murdoch et al. 1972, Nagel 1979, Siemann et al. 1998b). The results of this study support the latter argument.

One theme illustrated by the results of this study is that the effects of resource manipulations and disturbances at the base of the food web are more difficult to predict at the consumer level than at the producer (plant) level. The effects of haying and fertilization affect arthropod communities not only by altering the number and distribution of plant species available as hosts, and the total amount of plant biomass, but also by changing the availability of resources such as flowers and seeds. Such changes are not typically observed in studies of plant community dynamics, but as seen in this study, variations in the availability of these resources can create dramatic differences in the arthropod community. It is feasible, although beyond the scope of this study, that the June spike in grass seed abundance in hayed and especially hayed/fertilized plots might affect other groups of organisms besides the arthropods studied here. The grass seeds themselves might provide an enriched food source for granivorous rodents and birds, while the midges and wasps might support locally increased populations of insectivorous birds. It may be worth investigating whether larger areas of cool-season grassland in this region subjected to fertilization and haying support higher numbers of certain kinds of birds and mammals.

In conclusion, grassland arthropod communities are altered in abundance and diversity by management techniques such as fertilization and haying, but the specific effects observed depend on the time of year. NDVI is a useful predictor of ecosystem traits and biodiversity, and it is a surprisingly strong predictor of arthropod diversity.

Much of the variation in arthropod diversity that was not explained by NDVI was explained by grass seed abundance, which in this case was uncorrelated with NDVI. Using both ground-based and aerial techniques to monitor biodiversity is a promising approach not only for primary producers, but also potentially for higher trophic levels.

Table 2-1: Treatment effects on productivity variables (evaluated with ANOVA). F = significant main effect of fertilization; H = significant main effect of haying; F x H = significant fertilization x haying interaction.

Plant Responses	-Fert - Hay (mean)	-Fert +Hay (mean)	+Fert - Hay (mean)	+Fert +Hay (mean)	Significant sources of variation (P<0.05)
TINDVI	118.19	120.01	137.11	135.40	F
Biomass (g m^{-2})	155.89	140.72	396.10	491.88	F
Richness	31.38	34.13	18.00	28.00	F, H, F x H
Evenness	0.66	0.47	0.43	0.54	F x H
Shannon Diversity (H')	1.25	1.11	0.64	0.89	F, F x H
Seedheads per plot	11.75	22.44	5.87	50.00	F, H, F x H
Leaf % N	1.33	1.36	1.76	1.72	F
Leaf % C	41.3	41.1	42.9	42.9	F
Leaf C:N	31.20	30.21	24.46	25.24	F

Table 2-2. Treatment effects on arthropod community (evaluated with ANOVA). F = significant main effect of fertilization; H = significant main effect of haying; F x H = significant fertilization x haying interaction.

Arthropod Community Responses	-Fert - Hay (mean)	-Fert +Hay (mean)	+Fert - Hay (mean)	+Fert +Hay (mean)	Significant sources of variation (P<0.05)
June 2003					
Abundance	222.00	384.00	652.02	1080.13	F, H
Biomass (g m^{-2})	0.400	0.4037	0.916	0.5305	F
Richness	44.13	53.38	46.75	47.50	ns
Evenness	0.81	0.74	0.60	0.58	F
Shannon Diversity *(H′)*	1.33	1.28	1.01	0.97	F
August 2003					
Abundance	232.0	n/a	171.8	n/a	F
Biomass (g m^{-2})	3.141	n/a	3.764	n/a	ns
Richness	37.00	n/a	29.88	n/a	F
Evenness	0.38	n/a	0.37	n/a	ns
Shannon Diversity *(H′)*	1.33	n/a	1.19	n/a	F

Table 2-3: Correlations between response variables; arthropod data for June only. Top number in each cell is the correlation coefficient, bottom number is the P-value. * P<0.05, ** P<0.01, ***P<0.001.

	Arthropod Richness	Arthropod Mass	Arthropod Abundance	Plant Richness	Plant Biomass	Arthropod Evenness	Arthropod H'	Plant N (%)	Plant C (%)	# seed-heads	TINDVI
Arthropod Mass	0.166 0.365										
Arthropod Abundance	0.191 0.294	0.213 0.242									
Plant Richness	0.131 0.474	-0.600 0.000 ***	-.396 0.025 *								
Plant Biomass	-0.218 0.230	0.526 0.002 **	0.499 0.004 **	-0.876 0.000 ***							
Arthropod Evenness	-0.112 0.540	-0.366 0.060	-0.871 0.000 ***	0.544 0.001 **	-0.644 0.000 ***						
Arthropod H'	0.200 0.273	-0.279 0.121	-0.801 0.000 ***	0.563 0.001 **	-0.696 0.000 ***	0.949 0.000 ***					
Plant N (%)	-0.039 0.833	0.442 0.011 *	0.680 0.000 ***	-0.602 0.000 ***	0.800 0.000 ***	-0.694 0.000 ***	-0.694 0.000 ***				
Plant C (%)	0.097 0.599	0.361 0.042 *	0.537 0.002 **	-0.400 0.023 *	0.547 0.001 **	-0.644 0.000 ***	-0.600 0.000 ***	0.750 0.000 ***			
# seed-heads	0.049 0.791	-0.263 0.147	0.591 0.000 ***	0.229 0.208	-0.005 0.977	-0.397 0.025 *	-0.395 0.025 *	0.256 0.157	0.121 0.508		
TINDVI	-0.129 0.483	0.465 0.007 **	0.705 0.000 ***	-0.738 0.000 ***	0.883 0.000 ***	-0.859 0.000 ***	-0.859 0.000 ***	0.835 0.000 ***	0.702 0.000 ***	0.296 0.100	
Plant C:N	-0.109 0.552	-0.371 0.037 *	0.513 0.003 **	0.407 0.021 *	-0.523 0.002 **	0.627 0.000 ***	0.575 0.001 **	-0.682 0.000 ***	-0.982 0.000 ***	-0.090 0.624	-0.694 0.000 ***

Table 2-4a: Treatment effects on arthropod orders and morphospecies (evaluated with ANOVA). F = significant main effect of fertilization; H = significant main effect of haying; F x H = significant fertilization x haying interaction; ns = no significant effects

Arthropod Order and Morphospecies Responses	-Fert -Hay (mean)	-Fert +Hay (mean)	+Fert -Hay (mean)	+Fert +Hay (mean)	Significant sources of variation (P<0.05)
June 2003					
Orthoptera					
Abundance	23.38	71.00	36.38	52.00	H
Richness	4.00	5.50	3.50	2.88	F
Arachnida					
Abundance	12.87	19.63	10.25	19.63	H
Richness	5.63	5.13	4.38	4.75	ns
Coleoptera					
Abundance	4.13	11.75	6.63	45.75	F, H, FxH
Morphospecies D12	2.00	7.13	3.25	34.25	F, H, FxH
Richness	2.75	4.25	3.75	5.13	H
Heteroptera					
Abundance	2.63	5.38	5.75	21.38	F, H, FxH
Morphospecies F10	0.13	4.63	3.38	11.50	F, H, FxH
Richness	1.88	3.13	2.88	5.63	F, H
Homoptera					
Abundance	85.10	92.13	84.13	76.1	ns
Richness	10.25	12.38	9.00	7.63	F
Hymenoptera					
Abundance	28.50	62.40	173.60	582.00	F, H, FxH
Morphospecies B03	9.00	28.00	77.10	316.80	F, H, FxH
Morphospecies B31	7.25	23.60	88.50	232.60	F, H, FxH
Richness	8.13	10.50	8.25	8.63	ns
Diptera					
Abundance	61.30	114.30	255.00	230.60	F
Morphospecies G05	33.30	73.00	172.70	184.40	F
Richness	8.38	9.13	10.38	9.50	ns

Table 2-4b: Treatment effects on arthropod orders and morphospecies (evaluated with ANOVA). F = significant main effect of fertilization; H = significant main effect of haying; F x H = significant fertilization x haying interaction; ns = no significant effects

Arthropod Order and Morphospecies Responses	-Fert (mean)	+Fert (mean)	Significant sources of variation (P<0.05)
August 2003			
Orthoptera			
Abundance	53.63	53.75	ns
Morphospecies A04	15.25	14.13	ns
Morphospecies A17	8.00	7.38	ns
Morphospecies A08	9.00	6.88	ns
Richness	10.00	9.75	ns
Arachnida			
Abundance	67.00	61.80	ns
Morphospecies S03	25.00	12.63	F
Morphospecies S25	12.75	7.13	ns
Morphospecies S16	9.50	29.38	F
Richness	9.13	7.88	ns
Homoptera			
Abundance	53.13	11.13	F
Morphospecies C11	11.63	2.00	F
Morphospecies C12	12.38	0.75	F
Richness	10.63	5.63	F
Hymenoptera			
Abundance	6.13	7.63	ns
Richness	3.38	3.00	ns

Table 2-5a: PERMANOVA based on number of individuals in each species in June 2003

Source	*d.f.*	*S.S.*	*M.S.*	*F*	*P(perm)*	*P(MC)*
Fert	1	16796.89	16796.89	13.61	0.001	0.001
Hay	1	4433.72	4433.72	3.59	0.008	0.007
Fert x Hay	1	2532.31	2532.31	2.05	0.071	0.076
Residual	28	34563.93	1234.43			
Total	31	58326.86				

Table 2-5b: PERMANOVA a posteriori pairwise comparisons based on number of individuals in each species in June 2003

Comparison	Dissimilarity	*t*	*P(perm)*	*P(MC)*	# unique values
within - fert	56.22				
within + fert	44.12				
+ fert vs. - fert	66.56	3.48	0.001	0.001	998
within - hay	57.06				
within + hay	56.56				
+ hay vs. - hay	60.48	1.57	0.027	0.04	1000
within - fert within - hay	54.38				
within + fert within - hay	42.98				
+ fert vs. - fert within - hay	64.39	2.49	0.002	0.003	928
within - fert within + hay	55.48				
within + fert within + hay	32.88				
+ fert vs. - fert within + hay	66.83	3.12	0.001	0.002	925
within - hay within - fert	54.38				
within + hay within - fert	55.48				
+ hay vs. - hay within - fert	57.35	1.25	0.086	0.142	917
within - hay within + fert	42.98				
within + hay within + fert	32.88				
+ hay vs. - hay within + fert	49.53	2.27	0.002	0.005	920

Table 2-6a: PERMANOVA based on biomass of each species in June 2003

Source	*d.f.*	*S.S.*	*M.S.*	*F*	*P(perm)*	*P(MC)*
Fert	1	7974.39	7974.39	3.81	0.001	0.001
Hay	1	3920.45	3920.45	1.87	0.038	0.055
Fert x Hay	1	3632.09	3632.09	1.73	0.047	0.079
Residual	28	58635.41	2094.12			
Total	31	74162.33				

Table 2-6b: PERMANOVA a posteriori pairwise comparisons based on biomass of each species in June 2003

Comparison	Dissimilarity	*t*	*P(perm)*	*P(MC)*	# unique values
within - fert	68.09				
within + fert	61.38				
+ fert vs. - fert	70.39	1.90	0.001	0.001	998
within - hay	67.11				
within + hay	66.28				
+ hay vs. - hay	68.56	1.29	0.054	0.088	999
within - fert within - hay	67.06				
within + fert within - hay	58.78				
+ fert vs. - fert within - hay	70.77	1.69	0.006	0.023	924
within - fert within + hay	67.21				
within + fert within + hay	57.94				
+ fert vs. - fert within + hay	69.51	1.64	0.007	0.017	930
within - hay within - fert	67.06				
within + hay within - fert	67.21				
+ hay vs. - hay within - fert	68.93	1.16	0.165	0.220	917
within - hay within + fert	58.78				
within + hay within + fert	57.94				
+ hay vs. - hay within + fert	64.01	1.55	0.013	0.029	919

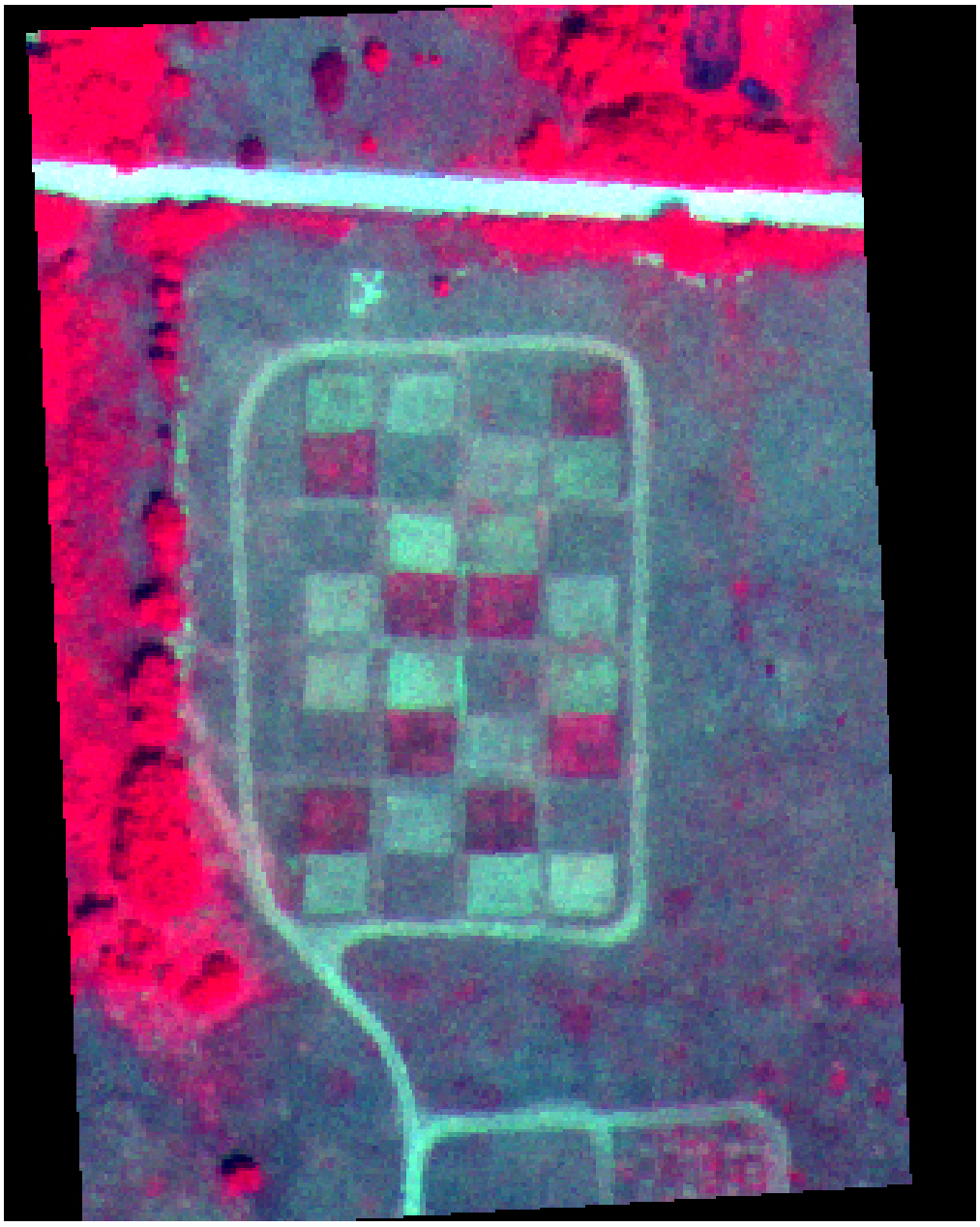


Figure 2-1. Multi-spectral image of the experimental landscape taken 3200 m ASL in June 2002 with a DuncanTech MS 3100 digital multi-spectral camera mounted in a single engine light aircraft. The experimental landscape is composed of 16, 10 x 20 m plots, each divided into two 10 x 10 m subplots.

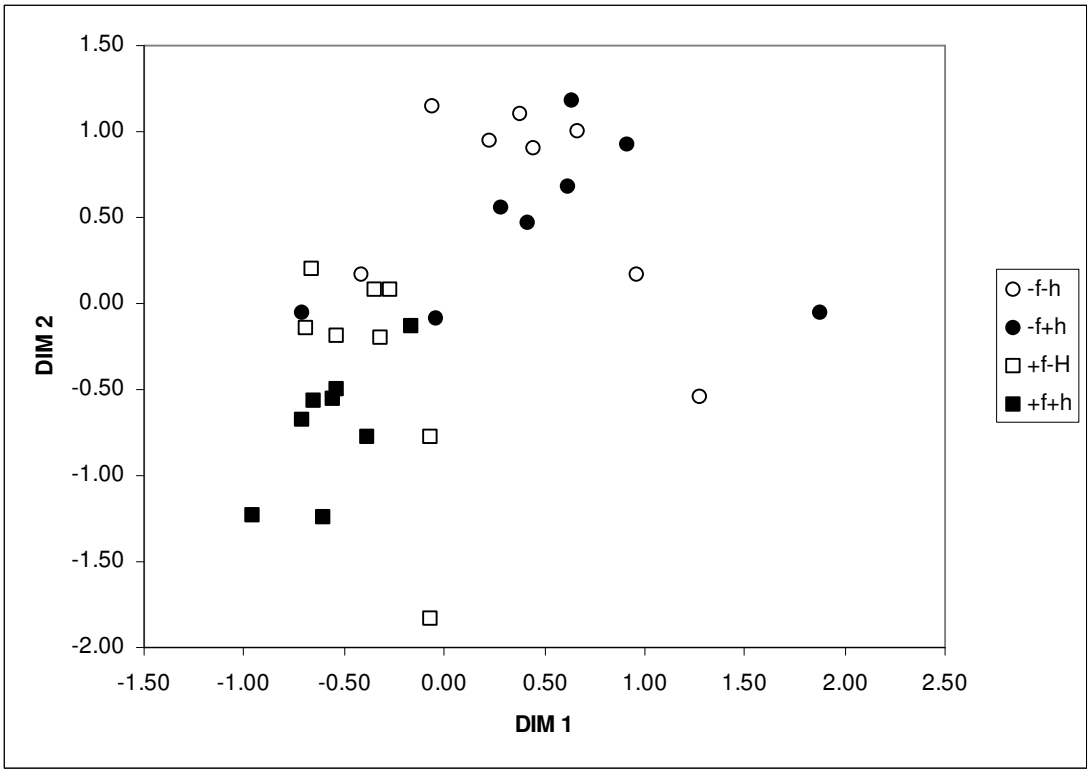
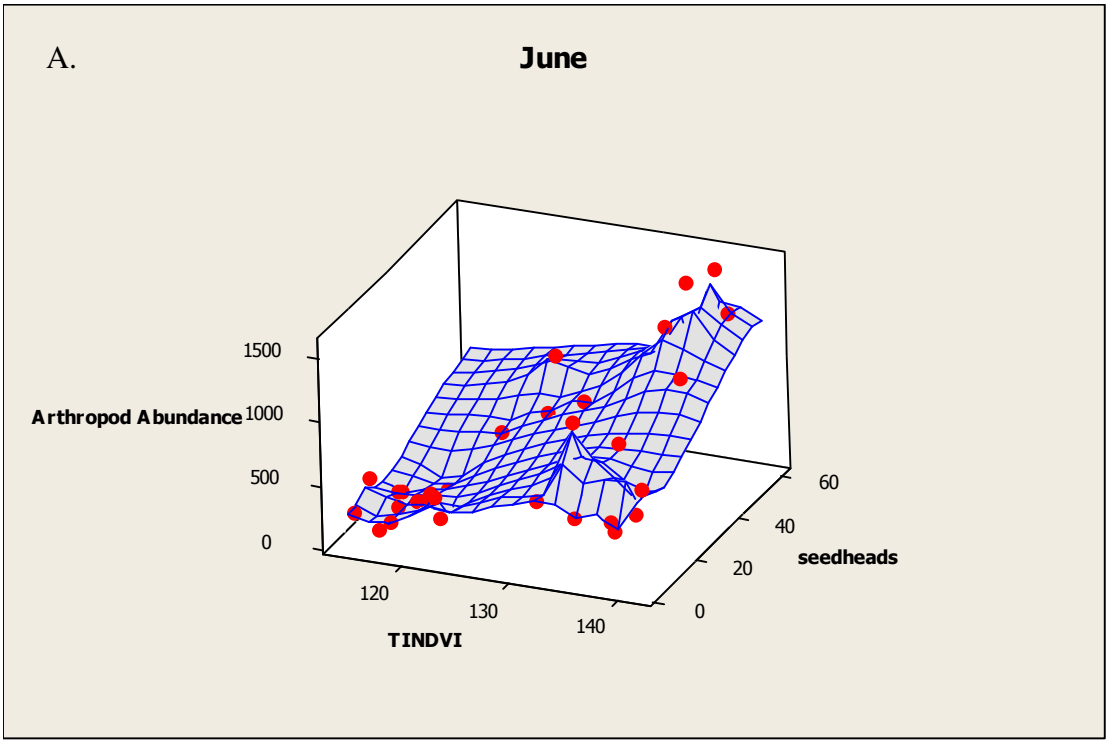


Figure 2-2: NMDS ordination based on Bray-Curtis dissimilarities from June 2003 arthropod species count data.

Figure 2-3: 3-D scatterplot of relationships between June arthropod abundance, TINDVI, and seedheads per plot. (A) shows that TINDVI and seedheads both correlate strongly with arthropod abundance, while (B) demonstrates that the four treatments tend to cluster together.

A.


June
Arthropod Abundance
1500
1000
500
0
120
130
140
TINDVI
0
20
40
60
seedheads

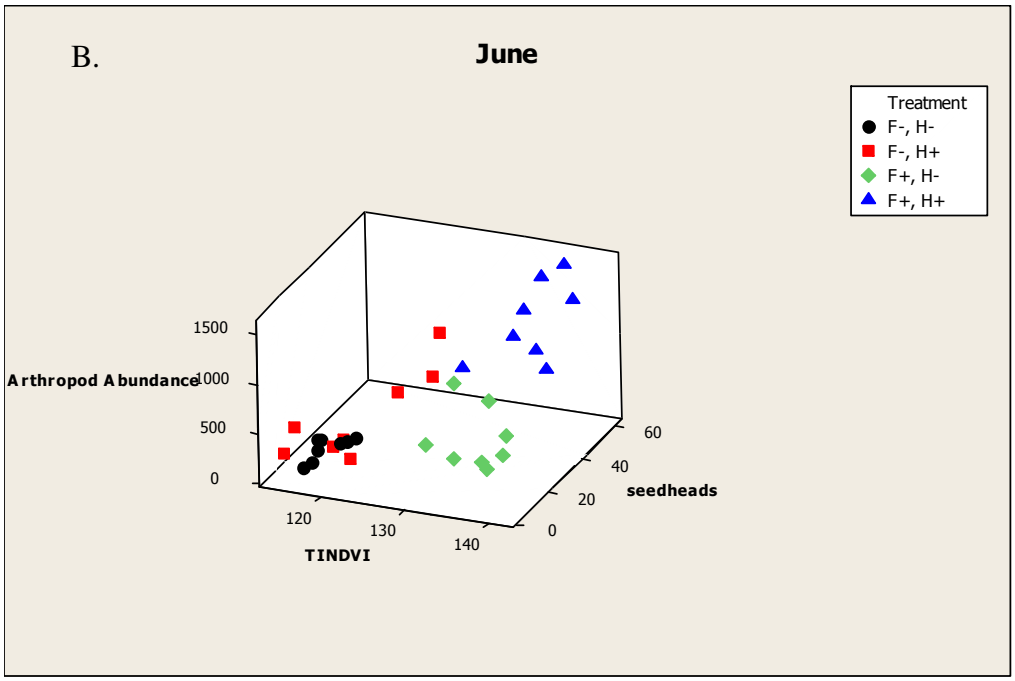
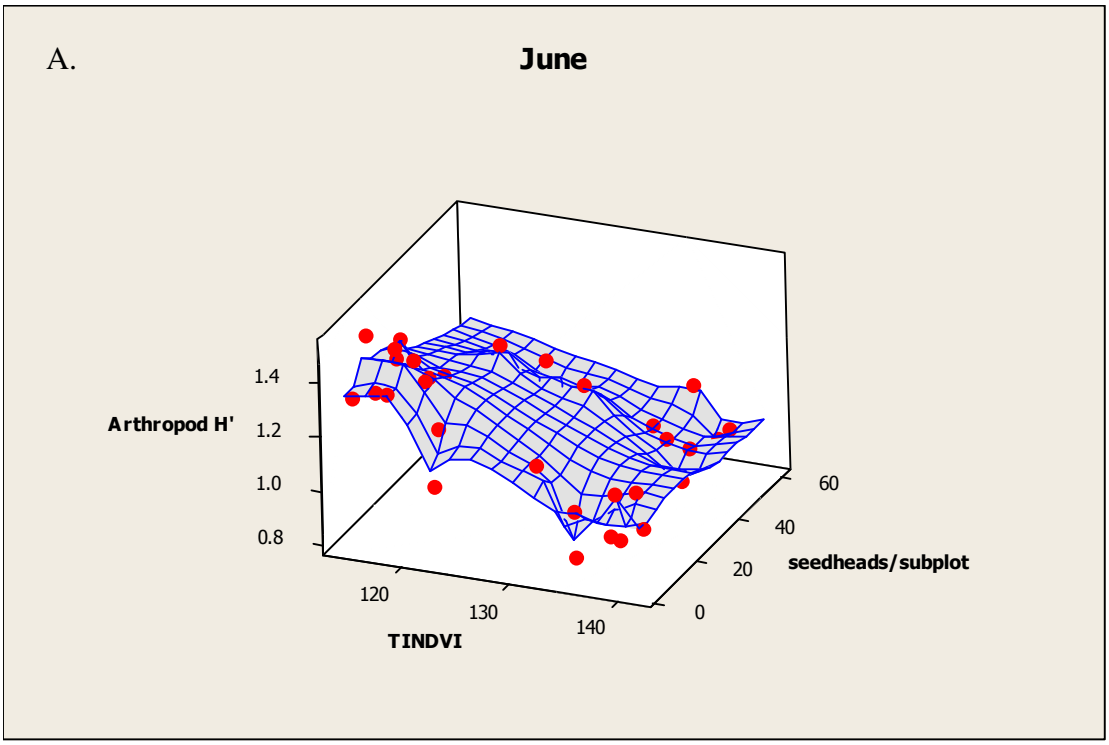
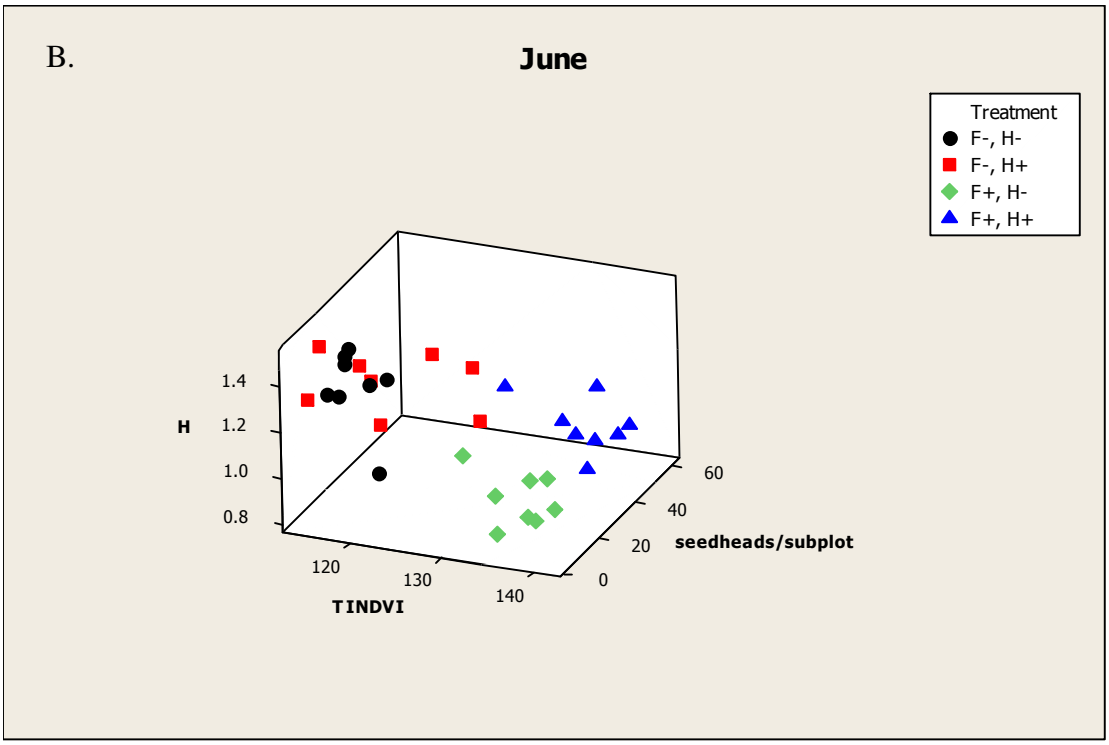

B.
June
Treatment
F-, H-
F-, H+
F+, H-
F+, H+
Arthropod Abundance
1500
1000
500
0
120
130
140
TINDVI
0
20
40
60
seedheads

Figure 2-4: 3-D scatterplot of relationships between June arthropod H', TINDVI, and seedheads per plot. (A) shows that TINDVI and seedhead abundance both correlate strongly with arthropod diversity (H'), while (B) demonstrates that the four treatments tend to cluster together.

A.


June
Arthropod H'
1.4
1.2
1.0
0.8
120
130
140
TINDVI
0
20
40
60
seedheads/subplot


B.
June
Treatment
F-, H-
F-, H+
F+, H-
F+, H+
H
1.4
1.2
1.0
0.8
120
130
140
TINDVI
0
20
40
60
seedheads/subplot

CHAPTER 3: ARTHROPOD AND PLANT RESPONSES TO HETEROGENEOUS AND HOMOGENEOUS NUTRIENT ENRICHMENT IN THREE PLANT COMMUNITIES

CHAPTER SUMMARY

Arthropod communities are shaped in large part by the plant communities in which they live and feed, but it is not understood how various characteristics of plant communities contribute to the formation of their associated arthropod assemblages. Some characteristics that are proposed to be of importance to arthropods include the type of plant species present, the number or diversity of plant species present, the nutritional quality or stoichiometry of plant tissues as a food source, the structure or "architecture" of plants as a part of the physical habitat, and finally, heterogeneity: the extent to which any or all of these attributes vary over a given spatial scale. Many ecological theories indicate that spatial heterogeneity of resources is a mechanism that maintains species coexistence and thus species diversity, but very few experiments have tested this theory, and none have focused on consumers. This study explores the relative effects of homogeneous and heterogeneous resource enrichment in herbaceous plant communities in central North America. Adjacent plant communities with different initial species composition and diversity received identical manipulations of nutrient availability, and the subsequent impact on the associated arthropod communities was examined. The results of this experiment suggest that arthropod abundance and diversity are determined more by plant species composition and diversity than by experimentally-imposed fluctuations in plant tissue quality, physical structure, or heterogeneity of any factor.

INTRODUCTION

A central goal of community ecology is to explain how biological communities are structured, and to predict how such communities respond to environmental change. Understanding the mechanisms that generate and maintain biological diversity in a particular habitat, taxon, or trophic level is the first step towards successfully managing that diversity, whether the intent is to preserve or to restore it. Both conservation and restoration become more crucial, and yet more difficult, as the pressures of human population growth on Earth's ecosystems becomes greater.

The quest to understand complex communities often begins with resources; all organisms need resources for growth and reproduction, and many are themselves resources for other organisms. Human activities have altered the cycling and distribution of many basic abiotic resources such as CO_2, phosphorus, and nitrogen (Vitousek et al. 1997b); as a result of human activities, atmospheric nitrogen deposition significantly increases nitrogen inputs to the soil (Vitousek et al. 1997a). Because of these anthropogenic changes, it is now more important than ever to understand how resource availability affects species, communities, and ecosystems.

This experiment explores the ways in which abiotic resource supply and heterogeneity of resources affect the species diversity of a consumer community. Arthropod communities in grasslands provide an interesting study system in which to manipulate the availability of an abiotic resource (nitrogen) to plants, and track the resulting changes in the consumer community. Tilman (1980) defines a resource as

"a factor which, through some range of availabilities, leads to higher population growth rates as its availability is increased and which is consumed, in the broad sense, by the population." For plants, resources are abiotic; nitrogen, phosphorus, light, and water are the ones that are most often limiting. For vegetation-dwelling arthropods, plants are the resources, and abiotic resources generally affect them indirectly, through the plants on which they shelter and feed or hunt prey.

Arthropods are an interesting group to study because of their great diversity and the complexity of their interactions with plants and with organisms in other trophic levels. They are also key components of many ecosystems, as herbivores, predators, parasites or parasitoids, prey, and detritivores. In certain systems, including some grasslands, arthropods eat more plant biomass each year than do vertebrate herbivores (Price 1997). They are a critical link in the cycling of nutrients and the flow of energy through terrestrial systems. From an anthropocentric perspective, arthropods are also commercially important as pests, pollinators, and predators in agricultural systems.

Nutrient Addition: Effects on Arthropods, Filtered Through Plants

There are several hypothetical mechanisms by which added resources could affect an arthropod community. The "consumer rarity hypothesis," also called the "more individuals hypothesis" in Srivastava and Lawton (1998),(Srivastava and Lawton 1998) states that adding resources will increase the total number of individuals (presumably through a greater supply of plant biomass and/or greater

nutrient content of plant biomass), thus making rare species more common and increasing the total number of species found in the community (Abrams 1995, Siemann 1998, Srivastava and Lawton 1998). The "resource rarity hypothesis" states that the diversity of plant species controls the diversity of arthropod species because higher plant diversity supports a greater number of specialist arthropods. Thus, a resource addition that boosts plant diversity will consequently increase arthropod diversity (Siemann 1998, Srivastava and Lawton 1998). The "density dependence hypothesis" states that adding resources will increase intraspecific density dependence, thus reducing interspecific competition. The usual mechanism proposed for this hypothesis is that specialized predators and parasitoids reduce the densities of otherwise dominant herbivore species (Abrams 1995, Siemann 1998, Srivastava and Lawton 1998). Each of these hypotheses makes predictions about the effects of nutrient addition on the arthropod community. Under the resource rarity hypothesis, productivity should increase herbivore species richness, there should be no significant relationship between herbivore abundance and herbivore species richness, and no significant effects of productivity on herbivore equitability (Siemann 1998). Under the consumer rarity hypothesis, productivity should increase herbivore abundance, but should not directly affect herbivore species richness except through its effects on abundance. Under the density dependence hypothesis, predators and parasitoids should increase, and there should be an increase in herbivore species equitability with increasing productivity. However, these three hypotheses and their predictions are

not mutually exclusive; all three could simultaneously contribute to the effects of nutrient enrichment on consumer communities.

Previous work has established that resource supply affects plant diversity; in most terrestrial herbaceous communities, an increase in nutrient supply leads to decreased diversity (Theodose and Bowman 1997, Grace 1999, Tilman et al. 2001). Although it is less thoroughly studied, there is also evidence that resource supply affects arthropod diversity (Murdoch et al. 1972, Kirchner 1977, Siemann 1998, Knops et al. 1999, Haddad et al. 2000, Marques et al. 2000, Brandle et al. 2001, Hartley et al. 2003). Whether the difference in arthropod diversity is attributable to differences in plant diversity or to more direct effects of nutrient addition varies among studies. Kirchner (1977) found an increase in arthropod diversity with short-term nutrient addition. Murdoch et al. (1972) found that Homoptera diversity was strongly correlated with plant species diversity and plant structure, measured by "foliage height diversity." Brandle et al. (2001) reported an increase in number of specialist herbivore species and abundance of specialists, correlated with an increase in plant species richness; however, there was no direct relation between productivity and carnivorous insect richness. Siemann (1998, Siemann et al. 1998) found that recent fertilization increased insect abundance and species diversity. Historical fertilization, which decreased plant species richness, increased insect species richness because of an increase in predators and parasitoids. Strauss (1987) found that fertilization of individual *Artemisia ludoviciana* plants increased the abundance and diversity of sucking insects found on them, but did not affect chrysomelid beetles.

Haddad et al., (2000) on the other hand, found that insect species richness decreased with long-term nitrogen addition, despite an increase in insect abundance. In a study by Vince et al. (1981), fertilization of marshes increased insect abundance in both high and low marsh environments, but increased insect diversity only in low marsh. Hurd and Wolf (1974) found that species richness increased early in the season in fertilized old-fields, mainly due to increased numbers of immature insects, and found little effect later in the season. In summary, experiments conducted in different systems, over different timescales, and following different methodologies have found a wide range of results.

Although it is clear that nutrient availability to plants affects the associated arthropod communities, it is unclear what attributes of the plant community cause these changes. Many of these experiments occurred over a period of more than three years, and the addition of nutrients to plant communities over that time span generally changes plant species composition in addition to changing the physical and physiological characteristics of the plants that are under treatment. Possible variables to which arthropods might respond include the number of plant species, the total living plant biomass, their nutrient content, their secondary chemistry, or their physical structure or "architecture." It is likely that arthropod diversity is influenced by many or all of these factors simultaneously. Nitrogen is shown to be a limiting factor for many arthropods, since arthropods have a much higher tissue N concentration than the foods which they eat (Mattson 1980, Joern and Behmer 1998, Elser et al. 2000a, Elser et al. 2000b, Fagan et al. 2002). However, different

herbivore species, even those that are within the same family, do not respond to higher dietary nitrogen in the same ways. For example, Joern and Behmer (1998) found that two grasshopper species responded differently to varying levels of nitrogen in their diets; one species showed decreased survival, and little reproductive response, while the other showed no change in survival, and an increased rate of reproduction. Some plants sequester nitrogen in their tissues when they have access to more of it; some of this extra nitrogen should be available to arthropods (Mattson 1980). Adding nitrogen also stimulates new plant growth, and growing tissue tends to be richer in available nitrogen (Mattson 1980, Crawley 1983). Plant biomass is another characteristic affected by addition of nutrients; more plant biomass means a higher abundance of food, and a greater amount of habitat, for arthropods. Plants may increase their physical or chemical defenses as more nutrients become available (Mattson 1980, Crawley 1983, Strong et al. 1984, Schoonhoven et al. 1998); alternatively, some plants may shift resources towards growth, reducing physical and chemical defenses. With added nutrients, plant "architecture," or physical structure, is often altered; this results in changes to microhabitat and availability of different plant parts for arthropods (Crawley 1983, Lawton 1983, Reid and Hochuli 2007) and can also change the dynamics of predator-prey interactions (Finke and Denno 2002). Finally, plant community composition changes in response to nitrogen addition over time (Grime 1979, Tilman 1987, Goldberg and Miller 1990, Theodose and Bowman 1997). Arthropod diversity is often related to plant diversity (Murdoch et al. 1972, Symstad et al. 2000, Brandle et al. 2001, Haddad et al. 2001, Jonas et al. 2002); thus,

the effect of nutrient enrichment on plant community composition would be expected to exert effects of its own, in addition to the previously listed, more direct changes.

Spatial Heterogeneity

Spatial heterogeneity of abiotic resources is proposed as a key factor allowing species coexistence within trophic levels (Tilman 1982, Naeem 1988, Tilman and Pacala 1993, Pacala and Tilman 1994). Among plant species, there are some that use resources very efficiently, and compete well at low growth rates, and some that can grow very quickly at high resource levels, but will be out-competed by more efficient growers at low resource levels. Thus, spatial variation in the availability of resources should promote the coexistence of plant species with differing strategies. However, the effect of spatial resource heterogeneity on diversity has had only a few empirical investigations at the producer level (Naeem 1988, Collins and Wein 1998, Baer et al. 1999, Stevens and Carson 2002), and none that focused on higher trophic levels. Hunter and Price (1992) propose a dominant role for plant heterogeneity in shaping the dynamics of arthropod populations and communities. Here, I hypothesize that both abiotic resource supply to plants, and the spatial distribution of resources, can influence arthropod communities in grasslands. There are multiple ways in which resource heterogeneity might be filtered through the plant community to affect arthropods: 1) more variance in the nutrient content of plant tissues, 2) more variation in physical structure (height, density) of plant "canopy", 3) altered plant species diversity and community composition, 4) more variation in secondary defense

compounds, 5) more variation in timing of growth, development, and seed set, 6) more variation in habitat resources and microclimates for both herbivores and their predators and parasitoids.

This experiment was designed to evaluate the effect of nitrogen fertilizer on arthropod communities in herbaceous plant systems. It explores how abiotic resource supply to plants, and heterogeneity of that resource supply, affect arthropod diversity and species composition in different types of plant communities. Three plant communities with different initial plant species diversity and composition were chosen, and each community received identical homogeneous and heterogeneous fertilization treatments.

Questions and Predictions:

1. How does (homogeneous) nutrient addition affect arthropod herbivore diversity?

- The *consumer rarity hypothesis* predicts that with increased resources (plant biomass, and plant tissue nutrient concentration) available to consumers, the number of individual arthropods will increase, and therefore the diversity of arthropod species will increase.
- The *resource rarity hypothesis* predicts that arthropod diversity will vary with plant diversity; if the number of plant species increases with nutrient addition, the number of arthropod species will increase. However, nutrient addition

often has the opposite effect, and decreases plant species diversity; in this case, arthropod diversity is predicted to decrease.

- The *density dependence hypothesis* predicts that increased resources should allow predators and parasitoids to exert stronger control over their prey populations. If the most competitively dominant herbivore species are the ones that are most reduced by predation, then interspecific competition should be reduced, and herbivore diversity should increase. In addition to a greater number of herbivore species coexisting, the reduction of dominant species should result in greater species evenness.

2. How do the effects of nutrient addition on arthropod diversity differ with the diversity and composition of the plant community to which the nutrients are added?

- The *consumer rarity hypothesis* predicts that in each plant community, the number of arthropod individuals will increase, and with it, the number of species. The initial plant diversity should not affect the outcome unless the more-diverse plant community contains more rare arthropod species that will benefit from the increase in numbers of individuals.
- The *resource rarity hypothesis* predicts that arthropod diversity will track plant diversity. Thus, if the effect of nutrient enrichment has a different impact on plant diversity in one community versus the other, the arthropod communities should respond accordingly. However, the resource rarity

hypothesis can be elaborated beyond plant species richness. Arthropods may be affected not only by the presence or absence of a host plant species, but also by its tissue quality, secondary compounds, reproductive state, and general architecture. In a more diverse plant community, we might assume that different plant species will have differing responses to nutrient addition; therefore, we might expect an additional increase in arthropod diversity.

- The *density dependence hypothesis* predicts that predation should exert more control over herbivores as nutrients are added. In a more-diverse plant community, there might be more species of predators and parasitoids already present; if this is true, then they should be better-positioned to increase along with their prey populations and exert control over potentially dominant prey species. It is also possible that in a more-diverse plant community, nutrient addition would be more likely to affect the abundance of a plant resource that predators or parasites need.

3. Does the effect of nutrient addition on arthropod diversity depend on whether the distribution of the added nutrients is homogeneous or heterogeneous?

- The *consumer rarity hypothesis* predicts that the change in arthropod numbers in the key factor; the distribution of the resources that cause the change in abundance should not matter. An exception to this might occur if patches that are highly enriched attract or support a disproportionately large number of arthropods; in other words, if the relationship between nutrients added and

number of arthropod individuals is not linear. Then, heterogeneous plots containing some highly enriched patches might harbor a greater number and greater diversity of arthropods than plots with homogeneous nutrient addition.

- The *resource rarity hypothesis* predicts that the effect on arthropod diversity will depend on the effects of enrichment on the number of resources offered by the plant community. If heterogeneity of nutrients increases plant diversity, or prevents the decrease that is often caused by homogeneous addition of nutrients, then arthropod diversity should respond similarly.
- The *density dependence hypothesis* seems to make no clear prediction about heterogeneity versus homogeneity of nutrient addition. Possibly, heterogeneity would increase the diversity of plant architecture, and the number of plant resources available to predators and parasitoids; this would make them more able to control prey populations.

4. Does the effect of nutrient heterogeneity on arthropod diversity depend on the initial diversity of the plant community?

- The *consumer rarity hypothesis* does not appear to predict an interaction; in heterogeneous plots with either high or low plant diversity, similar effects should be observed.
- The *resource rarity hypothesis* predicts that in a more-diverse plant community, heterogeneity might result in more plant diversity than homogeneous addition of nutrients, and therefore more arthropod species

should be found in a high-diversity, heterogeneously enriched plot than in a low-diversity, heterogeneously enriched plot. The greater numbers of plant species present also means that there will be a wider range of plant responses to nutrient addition, and thus a greater number of opportunities for arthropods.

- The *density dependence hypothesis* predicts that changes that benefit predators and parasitoids should increase the arthropod herbivore diversity. However, it is unclear whether nutrient heterogeneity would be more likely to benefit predators and parasitoids in a high-diversity or a low-diversity plant community. It is possible that heterogeneity in a high-diversity plant community would create a greater increase in diversity of plant structures, microhabitats, and plant resources, allowing a greater number of predator and parasitoid species to find niches.

MATERIALS AND METHODS

The experimental plots are located 12 kilometers north of Lawrence, Kansas, USA (Kettle and Whittemore 1991) at the Nelson Environmental Study Area (Jefferson County, 39˚03′ N, 95˚12′ W) in a former pasture/hay field. This tract of land is in the deciduous forest-tallgrass prairie ecotone, and consists of undulating ridge-to-swale geomorphology. The soil is Pawnee clay loam (fine, montmorillonitic, mesic Aquic Argiudolls), formed from glacial deposits of loess and till with weathering of interbedded limestones and shales (Kettle and Whittemore 1991). The

mean annual precipitation is 930 mm and the mean annual temperature is 12.9˚C (Atmospheric Science Library 1990).

Three sets of plots were established in 2004 to test the effects of fertilization in different plant community types, and to explore the ecological effects of patchy versus homogeneously-applied fertilization. Site 1 was located in an old-field dominated by *Solidago canadensis* and *Apocynum cannabinum*, with a considerable diversity of other forbs and mostly cool-season grasses. Site 2 was located less than 30 meters from Site 1, but has a different plant community due to differences in management history. Site 2 is dominated by the grasses *Bromus inermis, Sporobolus asper, Andropogon virginicus,* and the forb *Euthamia graminifolia*. Site 3 is located approximately 1 km from Sites 1 and 2, and is dominated by *Festuca arundinacea* and *Bromus inermis* and has a low diversity of forb species.

Experimental design

Each of the three sites received identical experimental manipulations. Plots were 10m x 10m, and arranged in a 6 x 3 grid. There were two N-fertilization treatments and one control, with six replicates of each, for a total of 18 plots at each site. Each fertilized plot received 16 g/m^2 of nitrogen via ammonium nitrate fertilizer each April. Ammonium nitrate was used in order to manipulate nitrogen availability while leaving phosphorus and potassium levels unchanged. The homogeneously fertilized plots received an even distribution of fertilizer across the plot, whereas the heterogeneously fertilized plots were sub-divided into 25 patches measuring 2m x

2m. Five of those patches received no fertilizer, five received 8 g/m^2, five received 16 g/m^2, five received 24 g/m^2, and five received 32 g/m^2. The patches were arranged in a Latin square design. Thus, a heterogeneously fertilized plot received the same average amount of fertilizer as a homogeneously fertilized plot; it was simply distributed differently (Figure 1).

Arthropod sampling and processing

Arthropod samples were collected in mid-June 2004. June was chosen because another arthropod study from the same ecoregion and vegetation type found that June arthropod samples had greater abundance and species richness than samples taken at other times during the growing season (Jonas et al. 2002). Samples were collected with broad sweeps of a muslin insect net through the upper layer of vegetation, while walking in six transects across each 10x10 meter subplot (Figure 2). The sampling effort for each transect was 25 sweeps, or a total of 150 sweeps per plot. Because arthropod communities near the edge of plots might be more representative of those outside of plots than those of the plot interiors, an effort was made to stay 2 m from the edge of each plot. According to Ritchie and Tilman (2000), grasshopper community composition changed dramatically within 3 m of the edge of fertilized plots. After each transect was completed, the contents of the sweep net were transferred to a jar with ethyl acetate as a killing agent, and then each sample was placed into a zip-lock bag and frozen at -20°C. Later, samples were thawed and processed: plant material and detritus was removed, and arthropods were sorted first

by order, then by morphospecies. A morphospecies is defined as a distinct phenotype recognizable by external morphological characteristics; sorting arthropods by morphospecies for the purposes of estimating taxonomic diversity has been shown to yield data that overlaps the data generated by taxonomists by 86% or more (Oliver and Beattie 1996). A collection of voucher specimens was developed to improve the consistency of morphospecies designations. For simplicity, morphospecies are referred to as "species" hereafter. After sorting, identification, and enumeration, arthropods were dried for 3 or more days in a 70°C oven, and then weighed to obtain dry weight (biomass). Sampling by sweep net provides a broad selection of arthropods, but there is some bias involved. This method emphasizes vegetation-dwelling arthropods and under-represents other groups: fast-flying aerial insects, litter-layer dwellers, and soil arthropods (Evans et al. 1983, Siemann et al. 1998).

Vegetation data

At each site, data on vegetation height and plant species composition in each plot were collected in August 2004 and in September 2005. To obtain an estimate of average vegetation height, five parallel transects were established 2 meters apart in each plot. On each transect, vegetation height was measured at intervals of 1 meter, yielding a total of 50 height measurements from each plot. To obtain an estimate of the number of plant species present in each plot, and their relative abundances, I performed a thorough visual survey of each plot, and recorded the presence and approximate percent cover of each plant species observed.

Spectral imagery of each site was obtained from the Kansas Applied Remote Sensing program during July 2004, and a representative image is presented in Figure 3 to aid in visualizing plot layout, and to provide qualitative confirmation that fertilized treatments were different in plant tissue quality than control treatments.

Statistical analyses

Analysis of variance (ANOVA) was used to examine whether plant height, plant species richness, arthropod species richness, number of arthropods per sample, and arthropod biomass differed among treatments. Because there was variation in plant height and plant species richness that was independent of experimental manipulations, stepwise regressions were performed to examine the association between arthropod community responses (species richness, abundance, biomass) and plant community variables. To test whether the variability of plant height among plots differed at Site 1 versus Site 2, the standard deviation of height measurements was calculated for each plot, and a 2-sample T-test was performed. To test whether height measurements within plots differed between treatments, the standard deviations of heights from each site were treated as a population, and analysis of variance was used to assess whether treatments increased the variability of plant heights.

RESULTS

Plant height

At Site 1, plant height was not significantly affected by treatment in either 2004 or 2005. At Site 2, fertilized (both homogeneous and heterogeneous) plots had taller vegetation than control plots (control = 51.96, homogeneous = 75.21, heterogeneous = 68.69; Table 1) in 2004, but there were no significant differences in 2005. At Site 3, plant height responded positively to fertilization in 2004, but negatively in 2005 (Table 1).

Site 1 and Site 2 both showed an increase in the variability (as indicated by standard deviation from the mean) of plant height measurements within fertilized plots as compared with control plots, but there seemed to be no additional variability generated by heterogeneous as opposed to homogeneous application of fertilizer (Figure 4, $P = 0.01$ for both Site 1 and Site 2). Site 1 and Site 2 were comparable in height variability in 2004, but in 2005, Site 1 had greater variability among plots than Site 2 ($P = 0.017$).

Plant species richness

At Site 1, plant species richness decreased in fertilized plots, both homogeneous and heterogeneous, but this response was statistically significant only in 2006, the third year of the experiment (Table 1). A similar pattern was seen in 2005, but the magnitude of the differences between treatments fell just short of significance at the 0.05 level. At Site 2, there was no significant response of plant species richness to fertilization in any year, although the non-significant trend that

appears to be present matches the pattern seen at Site 1, in which fertilization decreases species richness, especially in the final year of experimental manipulation.

Arthropod Biomass

Arthropod biomass at Site 1 was not significantly affected by fertilization in 2004. Both the overall arthropod community and the taxonomic orders analyzed showed no significant response. Arthropod biomass data from Site 2 also contained no significant results for either the community or its component taxonomic groups. Regression analysis showed no response of total arthropod biomass to plant height or plant species richness at either site. Site 1 and Site 2 had significantly different mean arthropod biomasses (1.42 grams for Site 1 and 2.65 g for Site 2, $P = 0.0001$).

Arthropod Abundance

The Site 1 arthropod community did not respond significantly at the 0.05 level, but the trend suggested by the data is that arthropods were more numerous in control plots than in either type of fertilized plots. This is mainly due to the responses of two groups, the Homoptera ($P = 0.070$) and Arachnida ($P = 0.030$). The arthropod community at Site 2 showed no numerical response to nutrient manipulation, either taken as a whole or broken down into orders. Regression analysis showed no response of total arthropod abundance to plant height or plant species richness at either site. Comparing Site 1 and Site 2 in 2004, Site 1 had higher mean arthropod abundance (372 vs. 229, $P = 0.005$).

Arthropod Species Richness

Total arthropod species richness did not respond to experimental nitrogen addition at either Site 1 or Site 2. Regression analysis showed no response of arthropod species richness to plant height or plant species richness at either site. At Site 1, no taxonomic group responded significantly to treatments, but at Site 2 the Homoptera and arachnids were more speciose in homogeneously fertilized plots than control plots; Homoptera were also more species-rich in heterogeneously-fertilized plots, but arachnids were equally diverse in control and heterogeneous plots. Arthropod species richness averaged across all plots was greater at Site 1 than at Site 2 (47.47 vs. 37.83, $P = 0.001$).

DISCUSSION

Based on a single season of arthropod diversity data, it is difficult to draw conclusions about the effect of resource heterogeneity on arthropod communities. The arthropod data gathered were from the first year of the experimental manipulation. I had hypothesized that the first year may show responses based on plant tissue chemistry and not plant diversity, because plant diversity was not likely to change drastically in the first season of nutrient manipulation. However, there is little evidence from most of the arthropod taxa examined, or from viewing the community as a whole, that any changes in plant tissue chemistry were of great enough magnitude to affect arthropods communities in a consistent way.

The consumer rarity hypothesis, which predicted greater numbers of arthropods where resources were added, was not supported because the abundance of arthropods actually decreased at Site 1, and was not affected at Site 2. The resource rarity hypothesis cannot be tested without changes in plant diversity, which did not occur during the first season of the experiment; but Site 1, with its richer plant community, did have a more diverse arthropod community.

The lack of arthropod data from subsequent years, in which plant diversity changes can be seen, prevents a test of the other part of the hypothesis, which is that changes in plant diversity resulting from fertilization treatments should "cascade up" to the arthropod community, producing changes in the diversity and abundance of arthropods in those years.

Differences in arthropod biomass, numerical abundance, and species richness were much greater between sites than within sites. The boundaries of sites 1 and 2 were less than 100 meters apart, so any differences in arthropod community were more likely a result of plant community compositional differences than abiotic factors. Thus, it appears that at least during a short-term experimental manipulation, the differences imposed by fertilization treatment were able to cause only a few detectable changes in the arthropod community in either site. Probably the main changes imposed on the plant community during the first year of the experiment were not changes in species composition, but rather changes in tissue nutrient concentration and in plant productivity and structure (overall plant height, variability of plant height, and overall biomass). It appears that plant species composition and

diversity, over a broader spatial and/or temporal scale than the scope of this experiment, had much more influence on arthropod numbers, biomass, and richness than plant tissue nutrient concentration or plant structure.

Table 3-1: Plant Species Richness ANOVA

	Control mean	Homogeneous fertilizer mean	Heterogeneous fertilizer mean	Significance (*P* value)
Site 1				
Plant Species Richness 2004	34.83	28.50	34.67	0.121
Plant Species Richness 2005	30.00	24.33	25.83	0.059
Plant Species Richness 2006	37.33	30.33	29.00	**0.001**
Site 2				
Plant Species Richness 2004	27.00	25.83	27.33	0.827
Plant Species Richness 2005	22.33	17.67	21.50	0.062
Plant Species Richness 2006	27.33	23.50	22.83	0.365
Site 3				
Plant Species Richness 2004	16.83	15.83	14.67	0.52
Plant Species Richness 2005	11.00	9.83	8.83	0.232
Plant Species Richness 2006	11.17	10.00	8.67	0.07

Table 3-2: Plant Height ANOVA

	Control mean	Homogeneous fertilizer mean	Heterogeneous fertilizer mean	Significance (*P* value)
Site 1				
Plant Height 2004	70.23	88.16	75.88	0.072
Plant Height 2005	71.80	74.15	64.26	0.181
Site 2				
Plant Height 2004	51.96	75.21	68.69	**0.016**
Plant Height 2005	69.35	68.25	67.88	0.963
Site 3				
Plant Height 2004	36.94	47.83	47.71	**0.0001**
Plant Height 2005	75.26	55.79	53.941	**0.0001**

Table 3-3: Arthropod Biomass ANOVA (grams dry mass per sample)

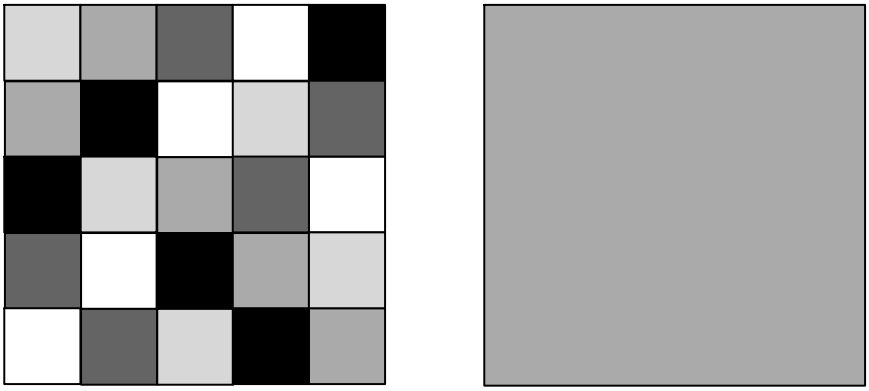
	Control Mean	Homogeneous Mean	Heterogeneous Mean	Signific-ance
Site 1				
Total Biomass	1.234	1.812	1.176	0.090
Orthoptera Biomass	0.775	1.347	0.763	0.067
Heteroptera Biomass	0.125	0.169	0.057	0.259
Coleoptera Biomass	0.099	0.128	0.147	0.624
Homoptera Biomass	0.124	0.091	0.096	0.499
Arachnid Biomass	0.111	0.077	0.122	0.919
Site 2				
Biomass	2.785	2.652	2.516	0.917
Orthoptera Biomass	2.582	2.324	2.135	0.759
Heteroptera Biomass	0.038	0.086	0.057	0.463
Coleoptera Biomass	0.036	0.016	0.151	0.360
Homoptera Biomass	0.070	0.118	0.106	0.362
Arachnid Biomass	0.058	0.107	0.067	0.233

Table 3-4: Arthropod Abundance ANOVA – number of individuals per sample

	Control Mean	Homogeneous Mean	Heterogeneous Mean	Significance
Site 1				
Total Abundance	492.70	311.50	301.40	0.077
Orthoptera Abundance	49.50	46.80	36.00	0.764
Heteroptera Abundance	81.30	96.00	41.40	0.439
Coleoptera Abundance	19.17	21.83	21.60	0.838
Homoptera Abundance	267.20	99.70	149.20	0.070
Arachnid Abundance	75.50	47.17	53.00	**0.033**
Site 2				
Total Abundance	218.80	246.80	221.70	0.896
Orthoptera Abundance	124.00	78.80	82.70	0.137
Heteroptera Abundance	12.00	25.80	19.83	0.691
Coleoptera Abundance	4.50	4.17	6.83	0.225
Homoptera Abundance	57.80	109.00	91.80	0.203
Arachnid Abundance	20.50	29.17	20.67	0.240

Table 3-5: Arthropod species richness ANOVA

	Control Mean	Homogeneous Mean	Heterogeneous Mean	Signifi-cance
Site 1				
Total Richness	47.50	47.67	47.20	0.997
Orthoptera Richness	6.67	6.33	6.40	0.948
Heteroptera Richness	8.50	8.67	8.20	0.946
Coleoptera Richness	8.83	9.83	9.40	0.901
Homoptera Richness	15.33	14.83	16.00	0.889
Arachnid Richness	8.33	8.00	7.40	0.702
Site 2				
Total Richness	35.33	39.50	38.67	0.436
Orthoptera Richness	8.50	6.83	7.17	0.258
Heteroptera Richness	3.50	3.67	4.50	0.668
Coleoptera Richness	2.83	3.17	4.00	0.442
Homoptera Richness	13.33	16.83	15.50	**0.031**
Arachnid Richness	7.17	9.33	7.67	**0.035**



A. **B.**

Figure 3-1: Application of fertilizer. A. Heterogeneously fertilized plot; levels of shading represent different rates of fertilizer application. B. Homogeneously fertilized; continuous shading represents consistent (homogeneous) application of fertilizer throughout plot.

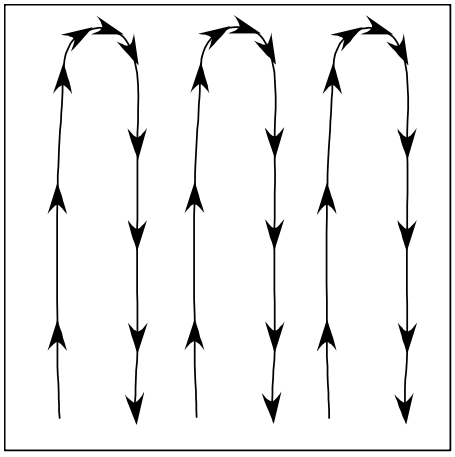


Figure 3-2: Transect pathways for sweep sampling within a plot.

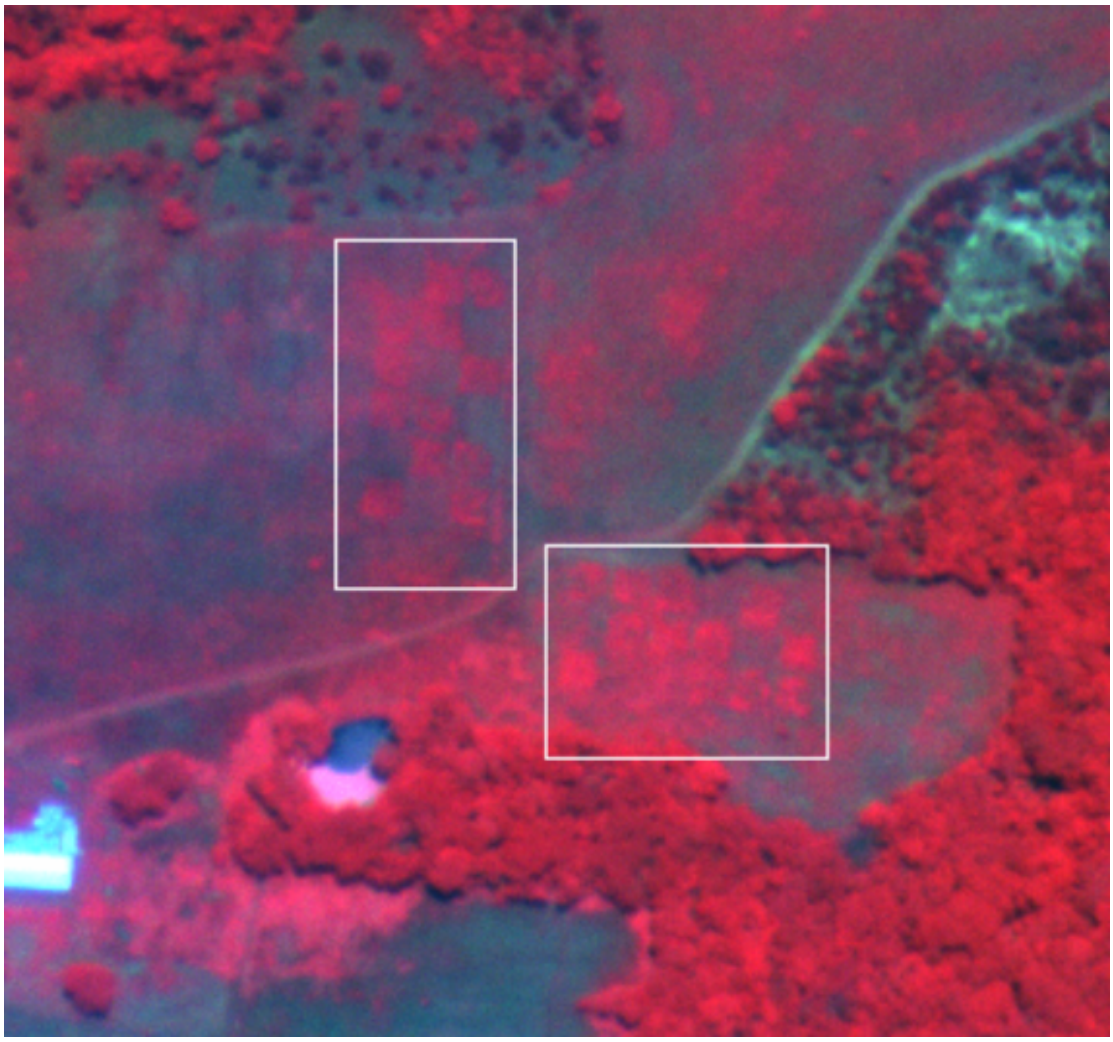


Figure 3-3: Spectral imagery of Site 1 (white rectangle on right) and Site 2 (white rectangle on left).

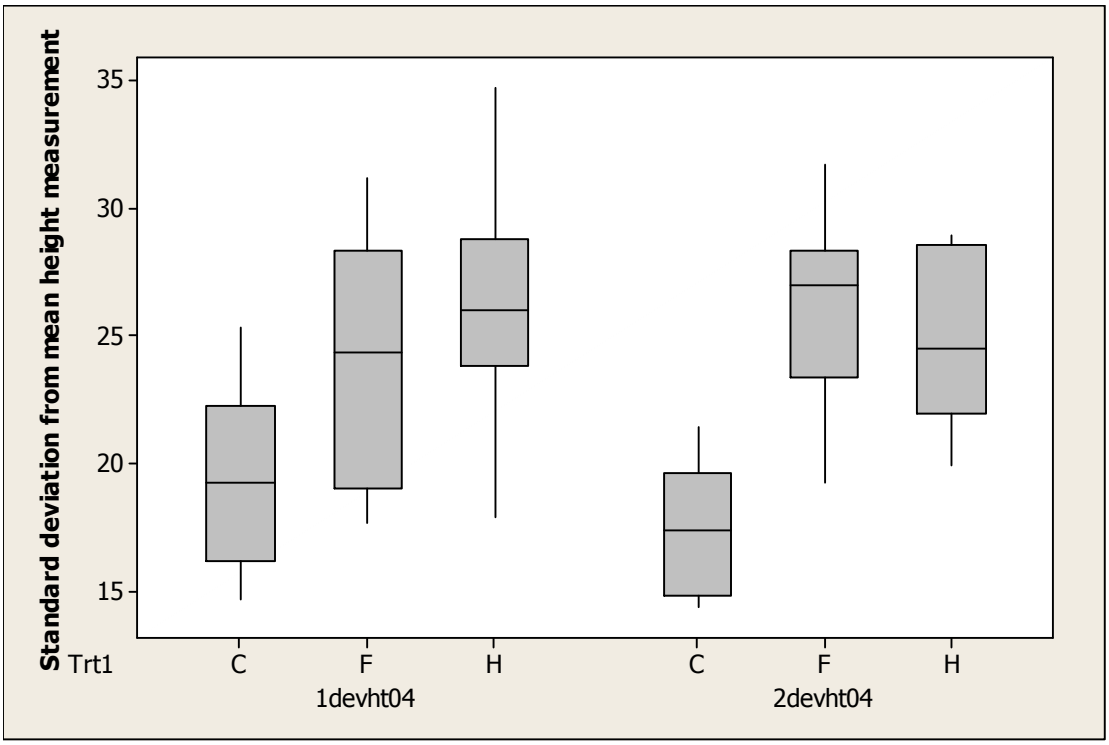


Figure 3-4: Plant height variability in 2004 for Sites 1 and 2.

GENERAL CONCLUSIONS

The insights from these experiments include both basic science and applied knowledge. The relationships between resources and their consumers, whether the resources are elemental nutrients, or primary producers (plants in this system), are rarely as simple as theoretical models predict, and the features specific to a species or a system often play a larger role than the generalities.

In these three experiments, the results of basal resource manipulation sometimes supported known theoretical patterns. In Chapter 1, the response of plant diversity to nitrogen appears to follow a unimodal curve – a diversity pattern that has often been observed along natural gradients, and about which much theoretical work has been written, but which is seldom seen in experiments. In Chapter 2, arthropod diversity responded to nutrient manipulation and disturbance in mostly predictable ways.

However, in both chapter 1 and Chapter 2, some of the responses of the manipulated communities were unexpected, and probably were related to the specific properties of the plant and arthropod communities of this system. In Chapter 1, the predicted response of the plant community to phosphorus addition did not materialize; phosphorus effects were observed only on one or two individual species, none of which were dominant in the community. In Chapter 2, the abundance of arthropods depended less on the abundance of plant biomass than on the abundance of grass seedheads, which were favored by haying and fertilization together, but only moderately by either treatment alone. The grass seedhead abundance was mostly

independent of plant biomass and TINDVI, which made it an interesting influence on arthropods. Also in this experiment, the response of the arthropod community was different in the early part of the growing season compared to later in the growing season; species richness and abundance were higher in fertilized plots than unfertilized plots in June, but the opposite was true in August.

Thus, one lesson of these experiments is one that many other ecologists have already noted, but deserves to be re-stated: things don't always react as predicted. In the world of plant and arthropod communities, plants and arthropods both respond to changes in nutrient availability and disturbance, but they don't always respond in the same direction. The species composition of an arthropod community is more changeable over a single growing season than that of the plant community upon which it is based; various arthropod groups and species tend to wax and wane over the course of a single season. As a result, the timing of arthropod sampling efforts may have a much greater impact on the resulting data and conclusions than the timing of plant community surveys in the same system.

Based on the results of Chapter 3, it appears that arthropods do not respond strongly to changes in plant tissue nutrient concentrations or plant biomass, but are more likely respond to changes in the abundance of different plant species and the availability of various plant-specific and time-specific resources such as fruit and flowers.

In sum, there is still much to be explored in the relationships between nutrient flows and ecological communities, particularly in the consumer trophic levels and the relationships between producer and consumer trophic levels.

WORKS CITED

Abrams, P. A. 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology **76**:2019-2027.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26**:32-46.

Anderson, M. J. 2005. PERMANOVA.

Averett, J. M., R. A. Klips, L. E. Nave, S. D. Frey, and P. S. Curtis. 2004. Effects of soil carbon amendment on nitrogen availability and plant growth in an experimental tallgrass prairie restoration. Restoration Ecology **12**:568-574.

Baer, S. G., J. M. Blair, and A. K. Knapp. 1999. Manipulation of soil resource heterogeneity in a tallgrass prairie restoration. Pages 78-87 *in* Proceedings of the North American Prairie Conference.

Baer, S. G., J. M. Blair, and A. K. Knapp. 2003. Soil resources regulate productivity and diversity in newly established tallgrass prairie. Ecology **84**:724-735.

Baer, S. G., D. J. Kitchen, J. M. Blair, and C. W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecological Applications **12**:1688-1701.

Bardgett, R. D., R. S. Smith, R. S. Shiel, S. Peacock, J. M. Simkin, H. Quirk, and P. J. Hobbs. 2006. Parasitic plants indirectly regulate below-ground properties in grassland ecosystems. Nature **439**:969-972.

Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. Ecological Applications **13**:605-615.

Board, J. E., V. Maka, and R. Price. 2007. Development of vegetation indices for identifying insect infestations in soybean. Agronomy Journal **99**:650-656.

Bobbink, R., M. Hornung, and J. G. M. Roelofs. 1998. The effects of airborne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. Journal of Ecology **86**:717-738.

Borges, P. A. V., and V. K. Brown. 2001. Phytophagous insects and web-building spiders in relation to pasture vegetation complexity. Ecography **24**:68-82.

Brandle, M., U. Amarell, H. Auge, S. Klotz, and R. Brandl. 2001. Plant and insect diversity along a pollution gradient: understanding species richness across trophic levels. Biodiversity and Conservation **10**:1497-1511.

Camill, P., M. J. McKone, S. T. Sturges, W. J. Severud, E. Ellis, J. Limmer, C. B. Martin, R. T. Navratil, A. J. Purdie, B. S. Sandel, S. Talukder, and A. Trout. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. Ecological Applications **14**:1680-1694.

Clay, D. E., K.-I. Kim, J. Chang, S. A. Clay, and K. Dalsted. 2006. Characterizing Water and Nitrogen Stress in Corn Using Remote Sensing. Agron J **98**:579-587.

Collins, B., and G. Wein. 1998. Soil heterogeneity effects on canopy structure and composition during early succession. Plant Ecology **138**:217-230.

Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology **76**:486-492.

Connell, J. H., and E. Orias. 1964. The ecological regulation of species diversity. The American Naturalist **XCVIII**:399.

Coops, N. C., M. Johnson, M. A. Wulder, and J. C. White. 2006. Assessment of QuickBird high spatial resolution imagery to detect red attack damage due to mountain pine beetle infestation. Remote Sensing of Environment **103**:67-80.

Copeland, T. E., W. Sluis, and H. F. Howe. 2002. Fire Season and Dominance in an Illinois Tallgrass Prairie Restoration. Restoration Ecology **10**:315-323.

Corbin, J. D., and C. M. D'Antonio. 2004. Can carbon addition increase competitiveness of native grasses? A case study from California. Restoration Ecology **12**:36-43.

Crawley, M. J. 1983. Herbivory: the Dynamics of Animal-Plant Interactions. University of California Press, Los Angeles.

Curry, P. S., R. P. Knowles, and J. Waddington. 1983. Seasonal occurrence and chemical control of the bromegrass seed midge, Contarinia bromicola (Diptera: Cecidomyiidae), in Saskatchewan. Canadian Entomology **115**:75-79.

De Cauwer, B., D. Reheul, S. De Laethauwer, I. Nijs, and A. Milbau. 2006. Effect of light and botanical species richness on insect diversity. Agronomy for Sustainable Development **26**:35-43.

Debano, S. J. 2006. Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona. Biodiversity and Conservation **15**:2547-2564.

Dennis, P., M. R. Young, and I. J. Gordon. 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology **23**:253-264.

Dickson, T. L. 2006. Species richness and composition: the varying importance of plant colonization along resource gradients. University of Kansas, Lawrence.

Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S. S. Kilham, E. McCauley, K. L. Schulz, E. H. Siemann, and R. W. Sterner. 2000a. Nutritional constraints in terrestrial and freshwater food webs. Nature **408**:578-580.

Elser, J. J., R. W. Sterner, E. Gorokhova, W. F. Fagan, T. A. Markow, J. B. Cotner, J. F. Harrison, S. E. Hobbie, G. M. Odell, and L. W. Weider. 2000b. Biological stoichiometry from genes to ecosystems. Ecol Letters **3**:540-550.

Eschen, R., H. Müller-Schärer, and U. Schaffner. 2006. Soil carbon addition affects plant growth in a species-specific way. Journal of Applied Ecology **43**:35-42.

Evans, E. W., R. A. Rogers, and D. J. Opfermann. 1983. Sampling grasshoppers (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: night trapping vs. sweeping. Environmental Entomology **12**:1449-1454.

Fagan, W. F., E. H. Siemann, C. Mitter, R. F. Denno, A. F. Huberty, H. A. Woods, and J. J. Elser. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. The American Naturalist **160**:784-802.

Fairbanks, D. H. K., and K. C. McGwire. 2004. Patterns of floristic richness in vegetation communities of California: regional scale analysis with multi-temporal NDVI. Global Ecology and Biogeography **13**:221-235.

Fay, P. A. 2003. Insect diversity in two burned and grazed grasslands. Environmental Entomology **32**:1099-1104.

Fielding, D. J., and M. A. Brusven. 1995. GRASSHOPPER DENSITIES ON GRAZED AND UNGRAZED RANGELAND UNDER DROUGHT CONDITIONS IN SOUTHERN IDAHO. Great Basin Naturalist **55**:352-358.

Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology **83**:643-652.

Fonseca, C. R., P. I. Prado, M. Almeida-Neto, U. Kubota, and T. M. Lewinsohn. 2005. Flower-heads, herbivores, and their parasitoids: food web structure along a fertility gradient. Ecological Entomology **30**:36-46.

Foster, B. L., and K. L. Gross. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. Ecology **79**:2593-2602.

Foster, B. L., C. A. Murphy, I. S. Khavin, M. Ramspott, K. Price, and K. Kindscher. submitted. Integrated effects of hay management on grassland diversity and ecosystem function: a field experiment.

Gibson, C. W. D., V. K. Brown, L. Losito, and G. C. McGavin. 1992. The response of invertebrate assemblies to grazing. Ecography **15**:166-176.

Gibson, D. J., T. R. Seastedt, and J. M. Briggs. 1993. Management practices in tallgrass prairie: large- and small-scale experimental effects on species composition. Journal of Applied Ecology **30**:247-255.

Goldberg, D. E., and T. E. Miller. 1990. Effects of different resource additions on species diversity in an annual plant community. Ecology **71**:213-225.

Gough, L., C. W. Osenberg, K. L. Gross, and S. L. Collins. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos **89**:428-439.

Gould, W. 2000. Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. Ecological Applications **10**:1861-1870.

Grace, J. B. 1999. The factors controlling species density in herbaceous plant communities: An assessment. Perspectives in Plant Ecology Evolution and Systematics **2**:1-28.

Grilli, M. P., and D. E. Gorla. 1997. The spatio-temporal pattern of Delphacodes kuscheli (Homoptera: Delphacidae) abundance in central Argentina. Bulletin of Entomological Research **87**:45-53.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature **242**:344-347.

Grime, J. P. 1979. Plant Strategies and Vegetation Processes. Wiley, New York.

Haddad, N. M., J. Haarstad, and D. Tilman. 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia **124**:73-84.

Haddad, N. M., D. Tilman, J. Haarstad, and J. M. H. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. American Naturalist **158**:17-35.
Hartley, M. K., W. E. Rogers, E. Siemann, and J. Grace. 2007. Responses of prairie arthropod communities to fire and fertilizer: Balancing plant and arthropod conservation. American Midland Naturalist **157**:92-105.
Hartley, S. E., S. M. Gardner, and R. J. Mitchell. 2003. Indirect effects of grazing and nutrient addition on the hemipteran community of heather moorlands. J Appl Ecology **40**:793-803.
Hartnett, D. C., and G. W. T. Wilson. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. Ecology **80**:1187-1195.
Heijden, M. G. A. v. d., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature **396**:69-72.
Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology **71**:478-491.
Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**:724-732.
Hurd, L. E., and L. L. Wolf. 1974. Stability in relation to nutrient enrichment in arthropod consumers of old-field successional ecosystems. Ecological Monographs **44**:465-482.
Hurd, L. E., L. L. Wolf, M. V. Mellinger, and S. J. McNaughton. 1971. Stability and diversity in three trophic levels in terrestrial successional ecosystems. Science **173**:1134-1136.
Huston, M. 1994. Biological Diversity: the coexistence of species in changing landscapes. Cambridge University Press, Cambridge, UK.
Joern, A., and S. T. Behmer. 1998. Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. Ecological Entomology **23**:174-184.
Jolivet, P. 1998. Interrelationships Between Insects and Plants. CRC Press, Boca Raton.
Jonas, J. L., M. R. Whiles, and R. E. Charlton. 2002. Aboveground invertebrate responses to land management differences in a central Kansas grassland. Environmental Entomology **31**:1142-1152.
Kettle, W. D., and D. O. Whittemore. 1991. Ecology and hydrogeology of the Kansas Ecological Reserves and the Baker Wetlands. Pages 91-135 Kansas Academy of Science Handbook. University of Kansas, Lawrence, Kansas.
Killham, K. 1994. Soil Ecology. Cambridge University Press, Cambridge, United Kingdom.

Kincaid, P., V. H. Smith, B. L. Foster, and V. L. Madden. 2002. Effects of phosphorus and nitrogen manipulations on tallgrass prairie restoration. Pages 364-369 *in* Forest and Conservation Nursery Associations.

Kirchner, T. B. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. Ecology **58**:1334-1344.

Kirkham, F. W., J. O. Mountford, and R. J. Wilkins. 1996. The effects of nitrogen, potassium and phosphorus addition on the vegetation of a Somerset peat moor under cutting management. Journal of Applied Ecology **33**:1013-1029.

Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. H. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecology Letters **2**:286-293.

Kruess, A., and T. Tscharntke. 2002a. Contrasting responses of plant and insect diversity to variation in grazing intensity. Biological Conservation **106**:293-302.

Kruess, A., and T. Tscharntke. 2002b. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. Conservation Biology **16**:1570-1580.

Lassau, S. A., G. Cassis, P. K. J. Flemons, L. Wilkie, and D. F. Hochuli. 2005. Using high-resolution multi-spectral imagery to estimate habitat complexity in open-canopy forests: can we predict ant community patterns? Ecography **28**:495-504.

Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology **28**:23-29.

MacArthur, R. H. 1965. Patterns of species diversity. Biological Reviews of the Cambridge Philosophical Society **40**:510-533.

MacArthur, R. H. 1972. Geographical Ecology. Harper and Row, New York, New York,USA.

Mamolos, A. P., D. S. Veresoglou, and N. Barbayiannis. 1995. Plant species abundance and tissue concentrations of limiting nutrients in low-nutrient grasslands: a test of competition theory. Journal of Ecology **83**:485-495.

Marques, E. S. D. A., P. W. Price, and N. S. Cobb. 2000. Resource abundance and insect diversity on woody fabaceous desert plants. Environmental Entomology **29**:696-703.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics **11**:119-161.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology **82**:2381-2396.

Morgan, J. P. 1994. Soil impoverishment: a little-known technique holds promise for establishing prairie. Restoration and Management Notes **12**:55-56.

Morghan, K. J. R., and T. R. Seastedt. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. Restoration Ecology **7**:51-55.

Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology **53**:819-829.
Murphy, C. A. 2004. Plant diversity and soil characteristics of managed grasslands in Northeastern Kansas. University of Kansas, Lawrence, Kansas.
Naeem, S. 1988. Resource heterogeneity fosters coexistence of a mite and a midge in pitcher plants. Ecological Monographs **58**:215-227.
Nagel, H. 1979. Analysis of invertebrate diversity in a mixed prairie ecosystem. Journal of the Kansas Entomological Society **52**:777-786.
Ojima, D. S., W. J. Parton, D. S. Schimel, and C. E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems. Pages 118-132 *in* S. L. Collins and L. L. Wallace, editors. Fire in North American Grasslands. University of Oklahoma Press, Norman, Oklahoma.
Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: A case study. Conservation Biology **10**:99-109.
Pacala, S. W., and D. Tilman. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. American Naturalist **143**:222-257.
Packard, S., and C. F. Mutel. 1997. The Tallgrass Restoration Handbook: for prairies, savannas, and woodlands. Island Press, Washington, D.C.
Perner, J., W. Voigt, R. Bahrmann, W. Heinrich, R. Marstaller, B. Fabian, K. Gregor, D. Lichter, F. W. Sander, and T. H. Jones. 2003. Responses of arthropods to plant diversity: changes after pollution cessation. Ecography **26**:788-800.
Perner, J., C. Wytrykush, A. Kahmen, N. Buchmann, I. Egerer, S. Creutzburg, N. Odat, V. Audorff, and W. W. Weisser. 2005. Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European grasslands. Ecography **28**:429-442.
Peterson, V. L. 1998. Effects of Nutrient Enrichment on a Successional Tallgrass Prairie. University of Kansas.
Price, P. W. 1997. Insect Ecology. John Wiley & Sons, New York.
Raman, A., editor. 1997. Ecology and Evolution of Plant-Feeding Insects in Natural and Man-Made Environments. International Scientific Publications, New Delhi.
Reid, A. M., and D. F. Hochuli. 2007. Grassland invertebrate assemblages in managed landscapes: Effect of host plant and microhabitat architecture. Austral Ecology **32**:708-718.
Ritchie, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. Ecology **81**:1601-1612.
Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.
Rothrock, P. E., and E. R. Squiers. 2003. Early succession in a tallgrass prairie restoration and the effects of nitrogen, phosphorus, and micronutrient enrichments. Proceedings of the Indiana Academy of Science **112**:160-168.
Rouse, J. W., R. H. Haas, J. Schell, and D. W. Deering. 1974. Monitoring vegetation systems in the Great Plains with ERTS.*in* Third Earth Resources Technology

Satellite-1 Symposium. Washington, DC, Greenbelt, MD: Goddard Space Flight Center, NASA SP-351, Science and Technical Information Office.
Samson, F. B., and F. L. Knopf. 1996. Prairie Conservation: Preserving North America's Most Endangered Ecosystem. Island Press, Washington, D. C. .
Sawyer, J. E., A. P. Mallarino, R. Killorn, and S. K. Barnhart. 2002. A general guide for crop nutrient and limestone recommendations in Iowa. Iowa State University Extension.
Schade, J. D., M. Kyle, S. E. Hobbie, W. F. Fagan, and J. J. Elser. 2003. Stoichiometric tracking of soil nutrients by a desert insect herbivore. Ecology Letters **6**:96-101.
Schoonhoven, L. M., T. Jermy, and J. J. A. v. Loon. 1998. Insect-Plant Biology. Chapman & Hall, London.
Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. Oecologia **87**:72-80.
Seastedt, T. R., and R. A. Ramundo. 1990. The influence of fire on below-ground processes of tallgrass prairie. Pages 99-177 *in* S. L. Collins and L. L. Wallace, editors. Fire in North American Grasslands. University of Oklahoma Press, Norman, Oklahoma.
Sedlacek, J. D., G. W. Barrett, and D. R. Shaw. 1988. Effects of nutrient enrichment on the Auchenorrhyncha (Homoptera) in contrasting grassland communities. Journal of Applied Ecology **25**:537-550.
Severns, P. M. 2003. Propagation of a Long-Lived and Threatened Prairie Plant, Lupinus sulphureus ssp. kincaidii. Restoration Ecology **11**:334-342.
Siemann, E. H. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology **79**:2057-2070.
Siemann, E. H., D. Tilman, J. Haarstad, and M. E. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. The American Naturalist **152**:738-750.
Smith, B., and J. B. Wilson. 1996. A consumer's guide to evenness indices. Oikos **76**:70-82.
Smith, M. R., I. Charvat, and R. L. Jacobson. 1998. Arbuscular mycorrhizae promote establishment of prairie species in a tallgrass prairie restoration. Canadian Journal of Botany **76**:1947-1954.
Smith, S. E., and D. J. Read. 1997. Mycorrhizal Symbiosis. Academic Press, New York, New York.
Smith, V. H., D. Tilman, and J. C. Nekola. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution **100**:179-196.
Soroka, J. J., and J. L. Nerland. 1992. Insects associated with seed heads of smooth bromegrass, Bromus inermis Leyss.*in* Joint Meeting of the Entomological Societies of Canada and Saskatchewan, Saskatoon, SK.
Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. The American Naturalist **152**:510-529.

Stevens, M. H. H., and W. P. Carson. 2002. Resource quantity, not resource heterogeneity, maintains plant diversity. Ecology Letters **5**:420-426.
Strauss, S. Y. 1987. Direct and indirect effects of host-plant fertilization on an insect community. Ecology **68**:1670-1678.
Strong, D. R., J. H. Lawton, and R. Southwood. 1984. Insects on Plants: Community Patterns and Mechanisms. Blackwell Scientific Publications, London.
Sudbrink, D. L., F. A. Harris, J. T. Robbins, P. J. English, and J. L. Willers. 2003. Evaluation of remote sensing to identify variability in cotton plant growth and correlation with larval densities of beet armyworm and cabbage looper (Lepidoptera : Noctuidae). Florida Entomologist **86**:290-294.
Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the United States of America **102**:4387-4392.
Swink, F., and G. Wilhelm. 1994. Plants of the Chicago Region. 4th edition. Indiana Academy of Science, Indianapolis.
Symstad, A. J., E. H. Siemann, and J. Haarstad. 2000. An experimental test of the effect of plant functional group diversity on arthropod diversity. Oikos **89**:243-253.
Theodose, T. A., and W. D. Bowman. 1997. Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. Ecology **78**:1861-1872.
Tilman, D. 1980. Resources: A graphical mechanistic approach to competition and predation. American Naturalist **116**:362-393.
Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.
Tilman, D. 1986. A consumer-resource approach to community structure. American Zoologist **26**:5-22.
Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs **57**:189-214.
Tilman, D., and S. W. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13-25 *in* R. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographic perspectives. University of Chicago Press, Chicago, Illinois.
Tilman, D., P. B. Reich, J. M. H. Knops, D. Wedin, T. Mielke, and C. L. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. Science **294**:843-845.
Tilman, D., and D. Wedin. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. Ecology **72**:685-700.
Tix, D., and I. Charvat. 2005. Aboveground Biomass Removal by Burning and Raking Increases Diversity in a Reconstructed Prairie. Restoration Ecology **13**:20-28.

Treseder, K. K., and M. F. Allen. 2002. Direct nitrogen and phosphorus limitation of arbuscular mycorrizal fungi: a model and field test. New Phytologist **155**:507-515.

Tscharntke, T., and H.-J. Greiler. 1995. Insect communities, grasses, and grasslands. Annual Review of Entomology **40**:535-558.

Turner, C. L., and A. K. Knapp. 1996. Responses of a C4 grass and three C3 forbs to variation in nitrogen and light in tallgrass prairie. Ecology **77**:1738-1749.

Van Dyke, F., S. E. Van Kley, C. E. Page, and J. G. Van Beek. 2004. Restoration Efforts for Plant and Bird Communities in Tallgrass Prairies Using Prescribed Burning and Mowing. Restoration Ecology **12**:575-585.

Verdu, J. R., C. E. Moreno, G. Sanchez-Rojas, C. Numa, E. Galante, and G. Halffter. 2007. Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. Biological Conservation **140**:308-317.

Vince, S. W., I. Valelia, and J. M. Teal. 1981. An experimental study of the structure of herbivorous insect communities in a salt marsh. Ecology **62**:1662-1678.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. Tilman. 1997a. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications **73**:737-750.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997b. Human domination of Earth's ecosystems. Science **277**:494-499.

Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. Annual Review of Systematics and Ecology **30**:257-300.

Wallis De Vries, M. F., A. E. Parkinson, J. P. Dulphy, M. Sayer, and E. Diana. 2007. Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity. Grass and Forage Science **62**:185-197.

Wedin, D., and D. Tilman. 1990. Nitrogen cycling, plant competition, and the stability of tallgrass prairie. Pages 5-8 *in* Twelfth North American Prairie Conference: Recapturing a Vanished Heritage, University of Northern Iowa, Cedar Falls.

Whiles, M. R., and R. E. Charlton. 2006. The ecological significance of tallgrass prairie arthropods. Annual Review of Entomology **51**:387-412.

Willems, J. H., R. K. Peet, and L. Bik. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. Journal of Vegetation Science **4**:203-212.

Wilson, S. D., and A. K. Gerry. 1994. Strategies for mixed-grass prairie restoration: herbicide, tilling, and nitrogen manipulation. Restoration Ecology **3**:290-298.

Wylie, B. K., E. A. Fosnight, T. G. Gilmanov, A. B. Frank, J. A. Morgan, M. R. Haferkamp, and T. P. Meyers. 2007. Adaptive data-driven models for estimating carbon fluxes in the Northern Great Plains. Remote Sensing of Environment **106**:399-413.

Zurbrugg, C., and T. Frank. 2006. Factors influencing bug diversity (Insecta: Heteroptera) in semi-natural habitats. Biodiversity and Conservation **15**:275-294.